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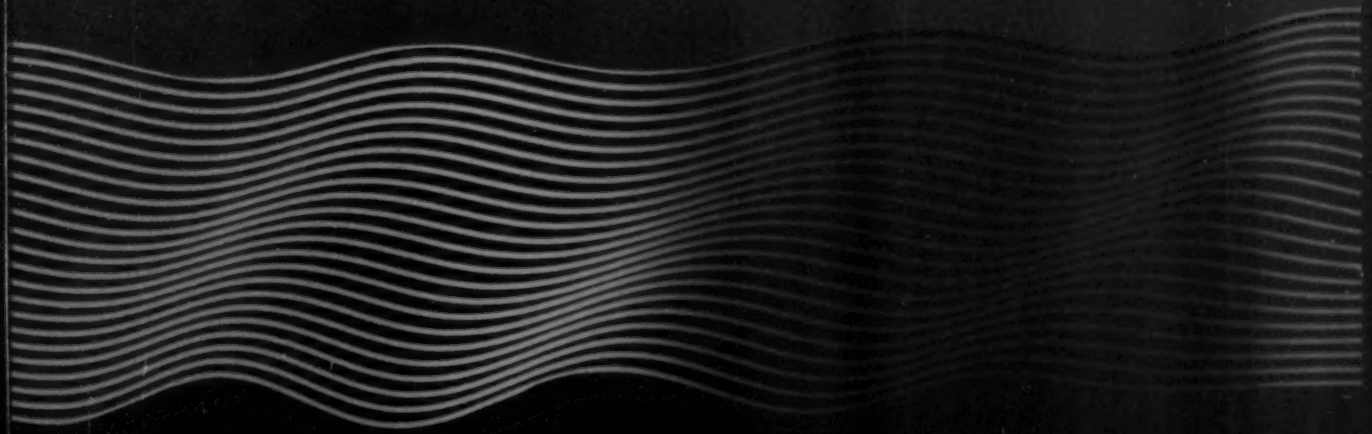

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Identifying the weakest link: simulating adaptive management of the reintroduction of a threatened fish

Andrew R. Bearlin, E.S.G. Schreiber, Simon J. Nicol, A.M. Starfield, and Charles R. Todd

Abstract: As part of an ongoing program of management for a critically endangered fish, we explored adaptive management as a method to overcome pervasive uncertainty regarding the reintroduction of trout cod (*Maccullochella macquariensis* Cuvier). We simulated the entire adaptive management cycle to explore the suitability of the approach for guiding threatened species management and to identify problems and barriers to "learning by doing". During the planning phase, a number of compromises were identified between specification of goals and objectives, the available management options, and current monitoring capacity. Undertaking a simulation of the implementation of alternate adaptive approaches to this reintroduction provided a number of insights into adaptive management in general. First, identifying the weak link in the process of inference emphasized the need to consider whether goals and objectives are achievable and meaningful and whether they complement monitoring and (or) any other limitations of the system. Second, in natural resource management, it is crucial to negotiate objectives in the light of what one can measure. Third, although there are lessons to be learned from each stage of the adaptive management cycle, there is value in simulating the entire adaptive management cycle, including management actions, monitoring, and the states of the system that lead to management intervention.

Résumé : Dans le cadre de notre programme de gestion des espèces sérieusement menacées, nous avons évalué la gestion adaptative comme méthode pour contrer l'incertitude omniprésente qui existe au sujet de la réintroduction du poisson percichthyidé *Maccullochella macquariensis* (Cuvier). Nous avons fait une simulation du cycle complet de la gestion adaptative pour déterminer l'efficacité de la méthode pour l'orientation de la gestion des espèces menacées et pour l'identification de problèmes et d'obstacles dans le processus d'«apprentissage par l'action». Durant la phase de planification, il a été possible de déceler plusieurs compromis entre l'énoncé des buts et des objectifs, les options de gestion disponibles et la capacité actuelle de surveillance continue. La mise en oeuvre simulée de plusieurs démarches de rechange pour la réintroduction de cette espèce a donné des perspectives intéressantes sur la gestion adaptative en général. Premièrement, l'identification des chaînons faibles dans le processus d'inférence met en relief la nécessité de voir si les buts et les objectifs sont réalisables et signifiants et s'ils sont des compléments à la surveillance et/ou aux autres lacunes du système. Deuxièmement, il est essentiel en gestion des ressources naturelles de confronter les objectifs à la lumière des mesures que l'on peut obtenir. Troisièmement, bien qu'il y ait des leçons à tirer de chacune des étapes du cycle de la gestion adaptative, il est intéressant de simuler le cycle au complet, y compris les interventions de gestion, la surveillance et les conditions du système qui suscitent des interventions de gestion.

[Traduit par la Rédaction]

Introduction

A reintroduction is the reinstatement of a population into an area that was historically part of the species range but from which it has become extinct. Reintroduction is a common management action for endangered species (IUCN 1996). In the Murray–Darling Basin in southeastern Australia, reintroduction of native fish and acclimatization of alien fish has been common practice since the early 1900s (Cadwallader and Gooley 1984; Cadwallader and Lawrence 1990). The critically endangered native trout cod (*Maccullochella macquariensis* Cuvier) were formerly distributed over a substantial portion of the Murray–Darling Basin, but have undergone a dramatic contraction in range (99%) in the last 50 years to the extent where the last unsupplemented indigenous population occupies a section of the Murray River approximately 200 km

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long (Douglas et al. 1994). The focus of recovery efforts has been to establish another self-sustaining population within the species' former range (Brown et al. 1998). To date, unsuccessful attempts have been made to reintroduce trout cod into 10 other river catchments (Douglas et al. 1994; Brown et al. 1998; Diver 1999) by releasing hatchery-produced fingerlings and yearlings (Brown 1998).

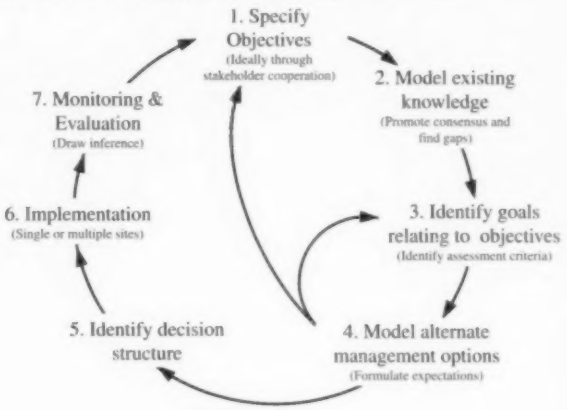
In general, reintroductions do not appear to be particularly successful for rare or threatened species (Griffith et al. 1989; Fischer and Lindenmayer 2000), particularly when "success" has been defined as the establishment of a self-sustaining population. This lack of success is often ascribed to an ad hoc approach to the pursuit of ill-defined goals (Fischer and Lindenmayer 2000). For trout cod it is likely that inappropriate release sites, poor release strategies (such as releasing small numbers of fish infrequently and irregularly through time), high mortality rates, and most likely, economic and organizational constraints have contributed to the failure in establishing self-sustaining populations (Brown et al. 1998; Todd 2001).

Successful species recovery would ideally be undertaken with a comprehensive ecological understanding of the threatened species and its response to management. In reality, this information is often not available and recovery actions invariably need to commence when knowledge, particularly that which would discriminate between competing management actions, is imperfect and uncertain. Adaptive environmental assessment and management (AEAM; Holling 1978), sometimes also called adaptive management (AM; Walters and Hilborn 1978; Walters 1986, 1997), is a management procedure that considers management alternatives as experimental treatments. AM brings to management the philosophy of the scientific method: management actions are implemented within a well-defined framework for setting goals, monitoring, and evaluation of outcomes (Walters 1986; Clark et al. 1995). Where possible, carefully constructed experimental controls and multiple treatments may be implemented. When controls and multiple treatments are impossible, as is the case in the example presented in this study, comparative management interventions may be designed and applied at the same temporal and spatial scale as management to test specific hypotheses related to particular management strategies (Cottingham et al. 2001). Consequentially, AM facilitates the methodical collection of information on how the ecology of the species and management interact.

Models play an important role in AM. Firstly, models provide a representation of the system itself and facilitate the formulation of hypotheses that logically precede learning. Secondly, models aid the development of cooperative and quantitative approaches to management (Starfield 1997). Thirdly, models are used to explore quantitative understanding of key components, relationships, assumptions, and uncertainty in the biological system. However, most importantly, models present a method for exploring the components of the entire management system, including decision rules, specific targets, contingencies, and alternate management strategies.

Generally, modeling is restricted to the quantitative biological aspects of an AM cycle (i.e., steps 2 to 4, Fig. 1). In marine fisheries management and conservation, management strategy evaluation and simulation have been advocated for several years (Sainsbury 1991; IWC 1994; Smith 1994). In contrast, in freshwater fish conservation, the consequences of simulating the management system and sociological elements, such as the implementation, monitoring, and evaluation stages, are rarely explored. This is particularly the case as applied here, where we seek to explore the decision process as well as optimize the capacity of the AM program to further our knowledge of the interaction between ecology and management of the system. Simulating the later stages of the AM cycle (Fig. 1) has several benefits. Simulating potential outcomes of an AM cycle given specific aims can help to assess whether, in the presence of uncertainty, the process is likely to provide the desired information with respect to these aims. By simulating a range of possible management decisions, we may explore and identify important factors in a management system and the compromises that may exist given multiple objectives.

Fig. 1. The adaptive management process. Common interpretations focus either on the outer loop, omitting iterative evaluation of hypotheses of the dynamics of the system and relevance to management objectives, or conversely, on the inner loops, omitting the steps allowing inference from management treatments.



In this study we explore whether the application of AM is likely to improve the prospects for reintroducing trout cod into parts of its former range. Given the assumption that with sufficient perseverance, efforts to establish a population must ultimately succeed, it follows that the key issues for a manager are those that relate to the short-term risk of failure through environmental stochasticity and to deployment of resources: (*i*) When is the population not growing as anticipated? (*ii*) How to establish this? (*iii*) When to implement an altered management strategy to achieve the population objective with available resources? We want to understand how environmental stochasticity and monitoring precision impact on management objectives and management options. Our aim was to determine the consequences of incorporating uncertainty in both monitoring and population dynamics in the modeling process and whether applying AM would allow early identification of unsuitable or ineffective management scenarios.

To explore these themes, we developed a hypothetical example: a recovery target of at least 8000 fish in a given location over 20 years was set and several realistic management strategies and monitoring programs were developed. We simulated the entire AM process to determine the consequences

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of reevaluating program objectives, release strategies, and measurement indicators and to identify any weak links in the process that would limit the capacity of the AM program to facilitate "learning by doing".

Methods

At each step of the AM cycle choices are made, e.g., between management interventions, goal formulations, and monitoring strategies. A strength of the AM process is that it is possible to explore a very large set of combinations of choices. Indeed a continuum of choices exists at each decision node. Therefore, to explore the sensitivity of the outcomes given various decisions, we focused on options at reasonable extremes of the range of possibilities. We used three stages of simulation to focus on distinct choices at each decision node (e.g., between reintroduction strategies, goal setting, monitoring, and risk profile) and, importantly, interactions between the various alternatives (Table 1). In addition to management choices, population growth rates are likely to be affected by uncertainty associated with ecological functions and processes. We simulated two underlying growth rates (λ) to explore the hypothesis that different states of the population would lead to different optimum management strategies. In stage 1 of our study, we explored reintroduction strategies, goals, and measurement endpoints in the context of perfect knowledge of the impact that management was having. Stage 2 explored the impact of imperfect information through the simulation of monitoring as it is currently applied. Stage 3 explored trade-offs between the optimal strategies emerging from stages 1 and 2 via a set of decision rules based on the risk profile of the manager. All three stages were simulated with two sets of underlying demographic parameters: high λ (an average population growth rate $\lambda > 1$) and low λ ($\lambda < 1$).

The population dynamics model used in the simulations (step 2 in Fig. 1) was a seven age–stage, discrete-time, stochastic population model developed for trout cod (Todd 2001) that incorporates environmental and demographic stochasticity in all aspects of the life history including recruitment and survivorship. Two alternate models were developed by modifying parameter values specified in the basic model (Todd 2001) to provide average geometric growth rates of approximately 0.98 (low λ) and 1.05 (high λ). All other basic parameters were unchanged. We performed 1000 iterations over a period of 20 years using a fixed random number seed so that comparisons could be made between simulations without added variation resulting from random initial conditions (i.e., environmental variation did not change between simulations). Catastrophes were simulated as total recruitment failure at least once in each simulation period with an average of twice in the 20-year simulation period. This was implemented by randomly selecting a year in which a catastrophe was certain as well as by allocating a probability of 0.1 that a catastrophe would occur in any other year. This led to a 95% confidence interval of 1,6 for the number of catastrophes in any given iteration.

In the first stage of simulations, we developed the reintroduction strategies and goal formulation in the context of environmental variation and catastrophes. Timetables for reintroduction of hatchery fish were postulated and implemented (Table 2). These strategies represented the same investment in terms of numbers of fish (80 000 fingerlings) but differed in timing, thereby contrasting aggressive strategies of stocking high numbers of individuals over a short period with conservative stocking of low numbers over a longer time frame. The outcomes of the 16 simulations (2 growth rates × 8 reintroduction strategies) were compared using several measures of performance: minimum population size (collected after reintroduction had ceased); probability of zero population size (P(total fail)); probability of being below a critical threshold (P(small), risk of being small, less than 600 adults or 2000 fish in total); and probability of being larger than a threshold population size (P(large), chance of being large, greater than 1000 adults or 6000 fish in total). These four measurement endpoints were assessed at years 10 and 20 of each simulation. These statistics were then used to compare the performance of the management strategies with respect to the likelihood of achieving the overall management goal. Different goal statements were made by applying comparative weights to each of the measurement endpoints (Table 3). For example, risky goal statements preferentially weighted the probability of attaining a large population early in the reintroduction project. Alternatively, conservative goal statements preferentially weighted high minimum population sizes over the long term and minimized the probability of total failure (Table 3). The simulations explored the expected benefit of establishing a population from staggering the release of fish, the cost of such a strategy in terms of lower ultimate population size, and the impact of the choice of performance measures in the presence of potentially unforeseeable catastrophes such as complete failure of recruitment.

In stage 2, simulations were performed to model the monitoring of abundance estimates of the population using electrofishing by boat. We postulated that if a manager knew that a catastrophe had occurred, then it would be reasonable to adopt or modify an appropriate strategy to counter this event. Abundance estimates made using electrofishing by boat are known to have errors associated with them (Pusey et al. 1998), and three different levels of variation associated with error in population estimates were simulated. A coefficient of variation (CV) of 20% represented monitoring at the highest level of accuracy, 50% represented an intermediate level, and 80% represented the lowest accuracy in monitoring. The hypothesis behind these differences was that monitoring accuracy is associated with different levels of resource allocation or effort. We simulated the trade-off between a less intensive (and hence possibly less effective) reintroduction strategy that left more resources for a more accurate monitoring program and vice versa. To reduce computational time, the eight reintroduction scenarios were reduced to five rational options (Table 4). Results from stage 1, that is, perfect knowledge, were used as baseline data against which population estimates generated from the simulated monitoring were compared. The likelihood of linking success to the prevailing strategy was calculated by recording the proportion of 1000 trials that correctly identified that the population was greater than a given size at a given time.

Finally, in stage 3, the adaptive trade-off between accuracy of feedback and effective reintroduction strategies was

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Table 1. Examples of the choices facing the manager at each decision node during the adaptive management process.

	Decision node		
Reintroduction strategies	Measurement endpoints	Monitoring design	Management risk profile
Few fish – long term	Large population	High effort – accurate	Risky
Many fish – short term	Small population	Low effort – inaccurate	Moderate
Combination[a]	Risk of failure	Medium effort	Conservative

[a]Some fish every other year.

Table 2. Different reintroduction strategies comprising variations of duration (years) and intensity (numbers of fingerlings), e.g., strategy 5 involves a reintroduction of 11 500 fish each year for 7 consecutive years.

Strategy	1	2	3	4	5	6	7	8
Years	1	2	4	5	7	8	10	10/2[a]
Numbers	80 000	40 000	20 000	16 000	11 500	10 000	8000	16 000

[a]16 000 fish stocked every 2nd year over 10 years.

Table 3. Measurement endpoints and weights.

		Weights		
Performance criteria		Conservative	Moderate	Risky
Time (year)	10	0.1	0.5	1
	20	1	0.5	0.25
Endpoint	Total population	0.5	0.5	0.5
	Adults	0.5	0.5	0.25
Measure	*P*(large)	0.1	1	1
	P(small)	0.75	0.75	0.25
	P(total failure)	1	0.5	0.1
	Minimum population size	1	0.5	0.1

Note: By allocating different weights to each of the endpoints, different expectations and goals can be specified. The individual values specified represent examples of possible goal statements and were chosen to reflect the relative importance of each measurement endpoint under each formulation. *P*(large), the probability population is greater than 1000 adults or 6000 in total; *P*(small), the probability population is less than 600 adults or 2000 in total; *P*(total failure), the probability population is zero.

Table 4. Stage 2 simulation options.

Growth rate (λ)	Reintroduction strategies	Monitoring strategies
High λ	80 000 × 1 year	20% CV
Low λ	40 000 × 2 years	50% CV
	20 000 × 4 years	80% CV
	16 000 × 5 years	
	16 000 × 5 over 10 years	

Note: CV, coefficient of variation.

explored further by contrasting two sets of decision rules. Two management "risk profiles" were constructed in terms of the values of the decision variables, such as target population sizes and variability of the monitoring program (and hence confidence in the estimated population size), that were triggers to implement an alternate strategy. The postulated "risk-averse" manager was characterized by conservative threshold population sizes (600 fish) and lower levels of certainty ($p = 0.5$), whereas the "risk-tolerant" manager nominated higher threshold populations (2000 fish) and higher levels of confidence in monitoring ($p = 0.8$) as trigger values warranting a change of strategy. To explore the two sets of management rules, an interactive simulation was written in S-Plus (MathSoft 1999) to contrast the alternate management styles of the "frequent fiddler" (making frequent small changes in response to less stringent rules for certainty) and the "big-bang" manager (making large changes only on the basis of certain information). The game consisted of the population dynamic model together with prompts for each input from the first two stages above. In each iteration of this interactive simulation, the manager was required to specify the allocation of resources to the reintroduction and the monitoring, nominate an expectation, act, monitor, and react according to the preset rules for post hoc confidence in the result. The decision facing the "virtual" manager was to choose between a series of actions concomitant with hypotheses of the probable status of the population. Consequently, performing many iterations and using decision rules described earlier, we looked for synergies between the monitoring and reintroduction strategies that were chosen and explored what impact the decision process of the manager had on the outcome of the entire process (Fig. 1, step 5).

Results

In stage 1 of the simulations, we compared the performance of a series of management actions, assessment endpoints, and goal formulations. Qualitative comparisons of the mean trajectories of 1000 stochastic projections revealed

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relatively small differences in the population sizes achieved under each of the strategies. In terms of average population sizes, the best- and worst-performing reintroductions differed by less than 20% after 20 years. Initial inspection showed that the most aggressive strategy performed best because of a greater number of adults maturing early in the simulation period. Although qualitatively similar, the differences between reintroduction strategies became evident when individual measurement endpoints were considered (Table 5). As expected, the more aggressive strategies (i.e., stocking larger numbers over short time frames) were most likely to perform well as measured by ambitious criteria such as *P*(large). However, aggressive strategies also incurred failure at a relatively high rate (Table 5). At the other end of the spectrum, the most conservative strategies were surprisingly poor performers, almost guaranteeing small populations. Also of note, contrary to our expectation, was that reintroducing fish five times over 10 years (every 2nd year) was a relatively unimpressive strategy (even incurring complete failure in five out of 1000 iterations), whereas the same release strategy over five consecutive years performed much better (Table 5). Introducing 16 000 fish each year for 5 years appeared to represent a good balance between sheer numbers and risk-spreading over the reintroduction period. After incorporating the weightings developed for the three risk profiles (Table 2), the management options were then ranked in terms of their performance (Table 6). Under a low-risk strategy, an 8-year reintroduction performed best, but as tolerance of risk increased, shorter reintroductions (with corresponding benefits in terms of performance) were preferred.

The inclusion of monitoring uncertainty in our simulations generally resulted in a low proportion of trials where monitoring correctly detected a population greater than 600 adults. This was most strongly related to the likelihood of achieving the goal given the differing strategies rather than as a function of either growth rate (λ) or reintroduction strategy (Table 7). This is reflected in the data for 4- and 5-year strategies, where it was observed that the proportion of correct detection was higher, although unresponsive to monitoring accuracy. The only significant interaction proved to be that of monitoring effort and time. Not surprisingly, the proportion of correct detection appeared to increase given more years for the population to grow and with more effort in monitoring.

In stage 3, we implemented the findings of the previous two stages in the interactive simulations. Because monitoring was unable to provide the required information on the status of the population at the first decision point (5 years), it was impossible to make a case for altering the reintroduction strategy. The management decision at the reintroduction strategy node was effectively reduced to finding the best-performing option (in terms of meeting the objective of the manager) that also suited the manager's risk profile. Ultimately, confidence in estimates resulting from monitoring was so low that any trade-off between the quality of information and improved population enhancement through differential resource allocation proved to be one-sided in the extreme. Regardless of the management profile, the decision of which reintroduction strategy to choose reverted to a basic optimization of the stocking strategy as performed in stage 1. This meant that each manager profile invested the minimum monitoring effort and adopted the strategy that was most likely to achieve the goals with a given level of risk tolerance.

Discussion

AM is a tool that aims to deal explicitly with uncertainty in natural resource management through a process of identification and analysis of critical aspects of management strategies (Walters and Hilborn 1978; Walters 1986). In this example of AM applied to a simulated reintroduction program, there is inherent uncertainty in the population sizes that could be achieved because of uncertain population dynamics and environmental variation. There is further uncertainty in the estimates of population abundance and even the effect of management actions. In this context we compared, via simulation, the various decisions that the manager would encounter throughout the entire AM cycle.

In stage 1 we explored reintroduction options and the methods of determining the optimum strategy given various interpretations of measurement endpoints, a range of goals, and a variable environment. In terms of the management problem at hand, we identified a trade-off between magnitude of the objective and the risk of failure. Mean trajectories of reintroduction scenarios showed that in the absence of catastrophes, large populations were the result of large numbers of fish released as soon as possible. As such, the apparent success of aggressive strategies is consistent with the concept of introduction success being correlated with propagule pressure (Williamson and Fitter 1996). Incorporating catastrophes and exploring high-, medium-, and low-risk goals, we found that the optimum strategies were those carried out over 4, 5, and 8 years. We found that in reducing the risk of total failure, we were forced to accept a lower probability of complete success and a corresponding lower outcome in terms of absolute numbers of adults. There is an obvious benefit to a risky strategy in that high targets may be reached, but there is still a reasonably large probability of complete failure owing to a catastrophe such as a complete recruitment failure in the year of introduction. Exploring strategies that minimized risk demonstrated that longer-term strategies reduce the chance of total failure (i.e., have minimum population sizes above zero), but at the price of smaller ultimate populations being more likely in the long term. Given this trade-off, a manager may ask: How long are reintroductions required before the risk of the population being below a low threshold is acceptably low? Alternatively, a manager may ask: What would be the optimum mix of timing and intensity to get the best of both strategies? The modeling experiments lead us to explore reintroduction options that were not initially identified. This is a clear benefit of the management evaluation approach (Smith 1994) and a key element of any adaptive strategy.

Logic would suggest that an aggressive strategy might become more attractive if monitoring could detect a recruitment failure and management could react. This leads one to look at the monitoring results. Current monitoring options simply do not adequately measure the consequences of any reintroduction scheme. The combination of environmental

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Table 5. Performance of each reintroduction strategy for each combination of performance measures, endpoints, and time frames.

			Strategy							
When (year)	Endpoint	Measure	1	2	3	4	5	6	7	8
10	All fish	*P*(large)	0.2	0.17	0.24	0.12	0.07	0.06	0.08	0.08
10	All fish	*P*(small)	0.5	0.48	0.54	0.51	0.6	0.61	0.37	0.5
10	All fish	*P*(total fail.)	0.25	0.16	0.04	0	0	0	0	0
10	All fish	Min. pop.	0	0	0	118	72	126	170	120
10	Adults	*P*(large)	0.17	0.15	0.12	0.14	0.1	0.06	0.03	0.03
10	Adults	*P*(small)	0.65	0.66	0.62	0.58	0.62	0.71	0.83	0.85
10	Adults	*P*(total fail.)	0.16	0.03	0.002	0	0	0	0	0.005
10	Adults	Min. pop.	0	0	0	70	20	40	48	0
20	Adults	*P*(large)	0.40	0.4	0.34	0.39	0.38	0.34	0.34	0.35
20	Adults	*P*(small)	0.57	0.5	0.48	0.46	0.44	0.46	0.52	0.45
20	Adults	*P*(total fail.)	0.35	0.16	0.08	0	0	0	0	0
20	Adults	Min. pop.	0	0	0	14	34	44	34	28

Note: *P*(large), the probability population is greater than 1000 adults or 6000 in total; *P*(small), the probability population is less than 600 adults or 2000 in total; *P*(total fail.), the probability population is zero (total failure); Min. pop., overall minimum population size after the completion of reintroduction.

Table 6. Relative performance of reintroduction strategies (a score of 1 being the optimum strategy under the each risk-weighted interpretation of the performance measures).

	Strategy							
	1	2	3	4	5	6	7	8
Low risk	0.07	0.42	0.52	0.84	0.98	1.00	0.84	0.88
Medium risk	0.60	0.76	0.70	1.00	0.79	0.63	0.64	0.56
High risk	0.97	0.89	1.00	0.82	0.46	0.29	0.41	0.31

and monitoring stochasticity is overwhelming. The nature of the sampling method combined with uncertainty about the ages of fish that are collected means that the apparent absence of a cohort in electrofished samples is not evidence that recruitment has failed. Within time frames of less than 5 years, it would not be possible to detect a complete recruitment failure in any particular year with any certainty, let alone gather data to interpret the dynamics of highly variable natural recruitment seen in this system. Given insensitive monitoring, it follows that conservative strategies look attractive, together with appropriately modified expectations and goals. This would minimize the probability of total recruitment loss (and hence total failure of the reintroduction), unless failure is associated with, for example, long droughts, successive years of very low recruitment, or some other unforseen catastrophe that acted over a prolonged period.

This exercise demonstrates that implementing an AM approach to this case study based on current management approaches would have failed in that no learning could have occurred. The results show that either monitoring techniques must be vastly improved or objectives of the program carefully stated, not because target population sizes may not be achievable, but because it would not be possible to tell whether they have actually been achieved. The combination of demographic, environmental, and monitoring stochasticity meant that managers could not link monitoring data to the likely success of any decision once the reintroduction strategy had been set. The limited capacity that managers have to manage adaptively reflects the high levels of uncertainty in all parts (biological and imposed) of the system they are trying to manage. In terms of AM, this argues strongly for a more active experimental, manipulative approach to exploring management options. Unfortunately, in this system and scale, with an endangered fish species, implementing multiple experimental "controls" and "replicates" is not possible. However, by exploring alternative approaches to structuring the goals and objectives of management, it remains possible to learn from the actions that must occur when managing for an endangered species. The management-modeling approach also provides a platform and the impetus for thinking about monitoring alternatives to evaluate in the future. For example, does a hybrid strategy (e.g., aggressive stocking with more time to assess effect) become an even stronger candidate if one has a conservative goal and analyses of the age structure of the fish caught during monitoring is conducted over several years? Or, alternatively, would the monitoring performance be improved if different batches of released fish carried distinguishing genetic markers? AM has the potential to help illustrate the impact that these issues and the underlying assumptions and demographic parameters (e.g., the effects of carrying capacity or predation and predator saturation) have on the decisions of managers.

We have developed several themes so far: firstly, current monitoring methods do not yield population estimates sufficient to discriminate between management hypotheses; secondly, modeling demonstrates that the cost associated with the inability to detect catastrophes is lower expectations from management actions; and thirdly, even if errors in population estimates could not be reduced, it is plausible that, given enough time, the ability to correctly conclude that a target had been reached would improve. This highlights the issue of the appropriate time frame for goal setting and assess-

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Table 7. Probability associated with correctly detecting that a target population size of 600 adults had been reached by given year under given growth conditions (λ).

		Monitoring strategy											
		Monitoring, CV = 80%					Monitoring, CV = 50%				Monitoring, CV = 20%				
Year	Reintroduction strategy	1	2	3	4	8	1	2	3	4	8	1	2	3	4	8
5	Low λ	0.076	0.069	0.045	0.204	0.043	0.210	0.237	0.222	0.287	0.213	0.297	0.356	0.262	0.304	0.339
	High λ	0.088	0.053	0.054	0.125	0.102	0.183	0.186	0.170	0.256	0.179	0.319	0.307	0.241	0.367	0.331
10	Low λ	0.080	0.159	0.506	0.031	0.207	0.214	0.249	0.548	0.131	0.258	0.299	0.370	0.519	0.272	0.350
	High λ	0.084	0.166	0.467	0.026	0.210	0.158	0.308	0.468	0.089	0.261	0.313	0.374	0.525	0.252	0.368
20	Low λ	0.023	0.411	0.753	0.068	0.055	0.171	0.477	0.715	0.208	0.188	0.225	0.479	0.726	0.275	0.259
	High λ	0.018	0.456	0.699	0.085	0.072	0.098	0.526	0.730	0.175	0.219	0.288	0.568	0.674	0.355	0.295

Note: CV, coefficient of variation.

ment. By manipulating elements of goal setting, such as longer time lines or alternate measurement endpoints, restating the goal can lead to a more robust strategy in terms of chance of success, but what are the implications for the other goals of AM? Without appropriate feedback we have simply optimized management to minimize risk. AM requires confirmation of success or failure to meet expectations (i.e., testing of hypotheses) to improve understanding and learn from unexpected events. Without the learning, a program of AM is better characterized as risk assessment (Maguire 1991) or management evaluation (Smith 1994).

Another observation arises from the exploration of the reintroduction strategies and monitoring efficacy. We have shown that the information from monitoring is relatively poor and at best related largely to the probability that a given reintroduction strategy achieves the target population. It follows that any AM design has to be planned over a time period that accounts for the biology of the subject and the capacity to detect the results of management actions. Even at year 20, given the most successful strategies, monitoring correctly detected success in approximately 60–70% of simulations. Consequently, it should be recognized that the reintroduction of a relatively long-lived species requires a long-term commitment, with an imperative for appropriate feedback (monitoring) along the way.

In the case of the reintroduction of trout cod, there were trade-offs identified at several stages of the process. We have concentrated on the practical options regarding how restating achievement criteria might reshape the decision about which strategy to choose and what alternative monitoring might offer. Given the restricted range of manipulative management options in this case, an attractive proposal may be to develop a spatial model and look for improved capacity in current methods of releasing fish and monitoring. Through such a strategy, an abundance-based measurement endpoint may possibly be avoided. Although such considerations are inevitably driven by policy and may take place on longer time scales, they are nonetheless important to consider and may reveal unexpected opportunities for improving the management of natural resources. This highlights a strength of the AM process in that it facilitates learning on institutional scales as well as on practical ones.

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Differential energy allocation of alternative male tactics in masu salmon (*Oncorhynchus masou*)

Yusuke Koseki and Koji Maekawa

Abstract: To compare energy allocation to gonad, relative to soma, between alternative male tactics (mature parr and migratory males) in masu salmon (*Oncorhynchus masou*), we quantified energy contents in somatic and testicular tissues for the two tactics from two lake-run populations (Shikaribetsu Lake and Shumarinai Reservoir) in Hokkaido, northern Japan. Mass-specific testicular energy ($kJ \cdot g^{-1}$) was lower in migratory males than in mature parr in the Shikaribetsu population, but not in the Shumarinai population. The consistent pattern was observed in somatic energy, suggesting that mass-specific energy reflects population environment rather than inherent allocation pattern. Despite this confounding effect of specific energy, total testicular energy (kJ), relative to total somatic energy, was higher in mature parr in both populations. We suggest that strong sperm competition involved with sneak spawning is responsible for an increased testicular investment in mature parr.

Résumé : Dans le but de comparer l'allocation de l'énergie aux gonades, relativement au soma, chez des mâles à stratégies reproductives différentes (tacons arrivés à maturité et mâles migrateurs) du saumon masou (*Oncorhynchus masou*), nous avons mesuré les contenus énergétiques des tissus somatiques et testiculaires chez des mâles des deux groupes dans des populations à reproduction lacustre (lac Shikaribetsu et réservoir Shumarinai) en Hokkaido, dans le nord du Japon. L'énergie spécifique à la masse ($kJ \cdot g^{-1}$) des testicules est plus élevée chez les mâles migrateurs que chez les tacons dans la population de Shikaribetsu, mais pas dans celle de Shumarinai. La même tendance s'observe dans l'énergie somatique, ce qui laisse croire que l'énergie spécifique à la masse reflète l'environnement plutôt qu'un pattern inhérent d'allocation. Malgré l'effet masquant de l'énergie spécifique, relativement à l'énergie somatique totale, l'énergie testiculaire totale (kJ), est plus élevée chez les tacons des deux populations. Nous croyons qu'une forte compétition spermatique combinée à une reproduction furtive est responsable de l'investissement énergétique testiculaire plus grand chez les tacons.

[Traduit par la Rédaction]

Introduction

Reproduction is a severely exhausting event in life for many organisms, and therefore reproducing organisms are often faced with energetic constraints. As a consequence, they may have to invest in current reproduction at the cost of future growth, survival, and reproduction (Roff 1992; Stearns 1992). In most cases, they may also have to allocate the finite energy to more than one reproductive task (e.g., intrasexual competition, courtship behavior, and parental care) at the time of reproduction (Wootton 1990). In theory, it is expected that selection favors the single pattern of energy allocation that maximizes individual fitness (Sibly and Calow 1986). Where individuals experience different selective pressure, different energy allocation patterns may evolve within populations.

Alternative male mating tactics may be a case where different energy allocation patterns occur. They typically include favored and disfavored tactics in terms of fertilization (e.g., fighter vs. sneaker). Theoretical models of sperm-competition games predict that disfavored tactics, compared with favored tactics, invest more into sperm for compensating the disadvantage in fertilization (Parker 1990*a*, 1990*b*). A number of empirical studies have showed the evidence that sneaker's sperm is superior to that of fighter or guarder in terms of its density, motility, fertilizing efficiency, and adenosine triphosphate (ATP) concentration (e.g., Gage et al. 1995; Simmons et al. 1999; Vladić and Järvi 2001). These superior sperm characteristics, especially the higher ATP concentration, may be achieved with higher energy expenditure. Thus, sneakers may allocate a higher energy to testes than guarders or fighters. Despite this potential effect of sperm competition, energy allocation to testes of alternative tactics has been poorly understood. The only study published to date is from polymorphic brown trout (*Salmo trutta*), where both males and females have small, resident forms and large, migratory forms in a population (Jonsson and Jonsson 1997). Jonsson and Jonsson (1997) showed that resident and migratory males have similar gonadosomatic indices (GSIs) in energy. However, this result may be not the typical case of energy allocation of alternative tactics because resident males may spawn not only as sneaker in the redd of migratory females, but also as fighter in the redd (nest) of resident females (Jonsson and Jonsson 1997).

In other migratory salmon populations, only males have alternative phenotypes, i.e., large adult male and small precocious male. In some Pacific salmon, these precocious

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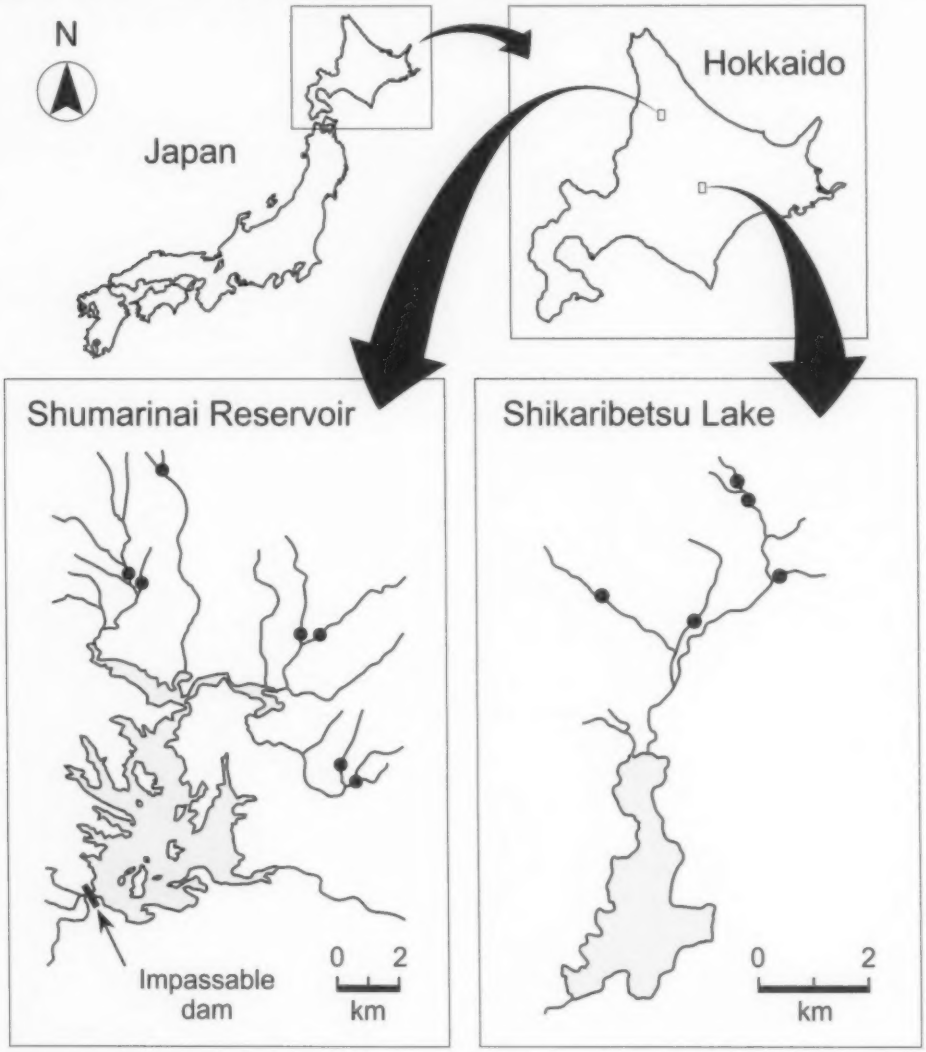
Fig. 1. Location of the two masu salmon (*Oncorhynchus masou*) populations studied: Shumarinai Reservoir (44°21′N, 142°13′E) and Shikaribetsu Lake (43°16′N, 143°07′E), Japan. Solid circles indicate the sampling sites.



males are known as jacks that return from the ocean 1 year earlier than other males and females (e.g., sockeye salmon (*Oncorhynchus nerka*; Foote and Larkin 1988) and coho salmon (*Oncorhynchus kisutch*; Gross 1985)). Jacks are semelparous like other adult migrants (Gross 1985). In other species, such precocious males are mature parr (e.g., Atlantic salmon (*Salmo salar*; Jones 1959) and masu salmon (*Oncorhynchus masou*; Koseki and Maekawa 2000)), which attain sexual maturity in the natal streams and show some potential for iteroparity (Tamate and Maekawa 2000*a*). Life-history switching from mature parr to migrants appears to be rare (0.1% of male smolts; Tsiger et al. 1994). Studies on spawning behavior have confirmed that although large migrants fight to get access to the female, mature parr and jacks sneak in the spawning of large migrants to fertilize some eggs (sockeye salmon jacks, Foote et al. 1997; masu salmon parr, Koseki and Maekawa 2000; Atlantic salmon parr, Jones and Hutchings 2002). As spawning by sneaking involves a dominant migratory fish and, in many cases, other conspecific individuals as well, mature parr and jacks are expected to experience, on average, higher levels of sperm competition than larger migrants.

Here, we first compare energy allocation between standard alternative male tactics, or mature parr and migrants, in masu salmon. Our prediction is that mature parr have a higher testicular energy relative to the somatic energy, as well as a relatively large testes mass for somatic mass.

Materials and methods

Sample collection

We studied masu salmon from two lake-run populations in

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Hokkaido, Japan: Shikaribetsu Lake (43°16′N, 143°07′E) and Shumarinai Reservoir (44°21′N, 142°13′E) (Fig. 1). The population in Shikaribetsu Lake originates from fish introduced in the 1980s and the Shumarinai population originates from native fish landlocked by damming in 1943 (Tamate and Maekawa 2000*b*). Lake-run masu populations are generally the same as anadromous populations in life-history characters including age compositions in mature parr, smolts, and adults and sex ratios in smolts and adults (Tamate and Maekawa 2000*a*).

On 26–31 August (for the Shumarinai population) and 2–4 September 1999 (for the Shikaribetsu population), mature parr and migrants were collected in several spawning streams (Fig. 1), using an electrofisher (model 12-B POW, Smith-Root Inc., Vancouver, Wash.). During sampling no redds were observed, nor were females with damaged caudal fins (resulting from redd construction) captured. Therefore, it is unlikely that our samples included fish that spent the sperm or energy for breeding activities. Moreover, gonadal developments of mature parr and migrants show similar temporal progression patterns with a peak about late August and early September, where the mean GSIs exhibit a slight change (8.1–10.6% for mature parr and 6.4–6.5% for migrants; see Sano 1947 and Utoh 1976). Thus, the observed difference in gonadal investment between mature parr and migrants is most probably the substantial pattern. All fish collected were immediately sealed in polyethylene bags and stored at –20°C until analysis.

Energy content

Energy contents in soma and testes were analyzed for 154 mature parr and 28 migrants from Shikaribetsu Lake and 88 mature parr and 11 migrants from Shumarinai Reservoir. After being partially defrosted, the fish were divided into testes and soma (all body parts excluding testes). Otoliths were extracted for age determination, and the consequent age compositions in the two populations were similar both for mature parr (age-0+, age-1+, and age-2+: Shikaribetsu, 51.3, 44.2, and 4.5%; Shumarinai, 60.2, 37.5, and 2.3%; $G = 2.25$, df = 2, $P = 0.33$) and for migrants (age-2+ and age-3+: Shikaribetsu, 89.3% and 10.7%; Shumarinai, 91.0% and 9.0%; $G = 0.02$, df = 2, $P = 0.88$). The separated soma and testes were weighed (nearest gram in the soma of migrants; otherwise nearest 0.01 g) and then homogenized using a meat grinder and blender. Within the two tactics, soma and testes of similar-sized individuals were sometimes pooled to obtain a sufficiently large sample for a series of analyses (~20 g).

From each homogenate sample, proximate composition (the main chemical constituents: water, ash, fat, and protein) was determined (proximate analysis; Brett 1995). We ignored carbohydrate because of its negligible amount in tissues of salmonid fishes (<0.1% in mean value; Jonsson and Jonsson 1997; Jonsson et al. 1997). Water was measured by freeze-drying about 20 g of each homogenate for 36 h (freeze dryer FD-5N, Tokyorikakikai Co., Tokyo, Japan). Ash was determined by combustion of 2 g dried samples at 550°C for 12 h. Fat was determined after extracting 2 g dried samples for 8 h with diethyl ether in a Soxhlet fat extractor (Tokyogarasukikai Co., Tokyo) (for the propriety of solvent and extraction time, see Dobush et al. 1985). Ash and fat proportions by dry mass were multiplied by the proportion of dry material in the original homogenate to translate into the proportions by wet mass. Protein proportion was estimated by subtracting the proportion of water, ash, and fat from 1 (Hendry and Berg 1999; Hendry et al. 1999). Mass-specific energy in soma and testes ($kJ \cdot g^{-1}$) were estimated by adding the proportions of fat and protein multiplied by the energy equivalents of 36.4 $kJ \cdot g^{-1}$ and 20.1 $kJ \cdot g^{-1}$, respectively (Brett 1995). Estimation of energy content using proximate analysis with energy equivalents is the standard approach in salmonid reproductive energetics (see appendix in Hendry and Berg 1999) and gives similar results to that using bomb calorimetry (Craig et al. 1978). Finally, total somatic and testicular energy (kJ) were calculated as the product of mass-specific energy and total mass in each tissue.

Data analysis

Before statistical analyses, proportion data (tissue constituents) were arcsine-transformed and data for energy and mass were $\log_{10}$-transformed. To examine the effects of alternative male tactics (A) and population (P) on the proximate composition and mass-specific energy in soma and testes, we first performed two-factor analysis of variance (ANOVA). However, because of the significant effect of the interaction between alternative tactics and population (A × P) in most of the analyses (see Results), we consequently tested the effect of alternative tactics by population using single-factor ANOVA. The testicular investment (mass or total energy) relative to somatic investment, or relative testicular investment, was compared among alternative tactics and populations using analysis of covariance (ANCOVA). The heterogeneity of the slopes of testicular investment on somatic investment (S) between alternative tactics (A) or populations (P) was tested in the full model including all interaction terms (S × A, S × P, A × P, and S × A × P). The effects of those interactions were not significant, indicating the homogeneity of slopes (see Results), and therefore were removed from the final model. As an intuitive and comparable measure of relative testicular investment (GSI, defined as the proportion of testicular investment to the somatic investment in this study) was calculated in terms of mass (g %) and energy (kJ %).

Results

Proximate composition and mass-specific energy

Two-factor ANOVAs revealed that the interaction between alternative male tactics and population had significant effects on the proximate composition and mass-specific energy of soma and testes (for water, ash, fat, protein, and energy in soma and water, protein, and energy in testes, all $P < 0.01$). Single-factor ANOVA by population showed that in Shikaribetsu Lake, proximate composition in soma differed completely between alternative tactics, including a higher water proportion and lower ash, fat, and protein proportions in migrants (all $P < 0.001$; Table 1). Specifically, the difference in fat proportion was as much as 2.2 times. Mass-specific energy in soma was significantly lower in migrants ($P < 0.001$). In Shumarinai Reservoir, proximate composition in soma was similar for alternative tactics (for water, fat, and protein, all $P > 0.30$), except that ash content was smaller in migrants

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Table 1. Comparison of proximate composition (% in wet mass) and mass-specific energy ($kJ \cdot g^{-1}$) in soma between alternative male tactics in the two masu salmon (*Oncorhynchus masou*) populations.

	Shikaribetsu Lake			Shumarinai Reservoir		
	Mature parr (68)	Migrants (28)	*F* value	Mature parr (44)	Migrants (11)	*F* value
Water	76.9 ± 1.0	79.2 ± 1.4	83.654*	78.1 ± 1.3	78.1 ± 0.9	0.006
Ash	2.6 ± 0.2	2.3 ± 0.4	19.065*	2.6 ± 0.2	2.0 ± 0.3	60.159*
Fat	2.6 ± 0.7	1.2 ± 0.9	76.459*	2.5 ± 1.0	2.9 ± 1.0	0.946
Protein	17.9 ± 0.5	17.3 ± 0.7	20.206*	16.8 ± 0.6	17.0 ± 0.4	1.075
Energy	4.5 ± 0.3	3.9 ± 0.4	65.549*	4.3 ± 0.4	4.5 ± 0.4	1.331

Note: Numbers of sample homogenates are given in parentheses. Values are mean ± standard deviation. All significance of *F* values were still held after correction for multiple comparisons by the sequential Bonferroni method (Rice 1989); *, $P < 0.001$.

Table 2. Comparison of proximate composition (% in wet mass) and mass-specific energy ($kJ \cdot g^{-1}$) in testes between alternative male tactics in the two masu salmon populations.

	Shikaribetsu Lake			Shumarinai Reservoir		
	Mature parr (18)	Migrants (17)	*F* value	Mature parr (9)	Migrants (10)	*F* value
Water	80.0 ± 0.9	81.6 ± 1.2	22.871*	78.5 ± 1.5	78.0 ± 1.3	0.529
Ash	2.9 ± 0.3	3.1 ± 0.3	3.025	3.3 ± 0.4	3.2 ± 0.3	0.002
Fat	1.5 ± 0.1	1.3 ± 0.1	18.196*	1.5 ± 0.1	1.4 ± 0.1	2.033
Protein	15.6 ± 0.9	13.9 ± 1.1	23.710*	16.8 ± 1.3	17.3 ± 1.3	0.922
Energy	3.7 ± 0.2	3.3 ± 0.2	27.668*	3.9 ± 0.3	4.0 ± 0.3	0.381

Note: Numbers of sample homogenates are given in parentheses. Values are mean ± standard deviation. All significance of *F* values were still held after correction for multiple comparisons by the sequential Bonferroni method (Rice 1989); *, $P < 0.001$.

Table 3. Analysis of covariance for the effects of alternative tactics (mature parr and migrants) and population (Shikaribetsu Lake and Shumarinai Reservoir) on testicular investment (total energy or wet mass), together with the covariate effect of somatic investment.

Testicular investment Source of variation	df	MS	*F*	*P*
Energy				
Somatic energy (S)	1	14.677	836.663	<0.001
Alternative tactics (A)	1	0.253	14.418	<0.001
Population (P)	1	0.389	22.179	<0.001
Error	277	0.018		
Mass				
Somatic mass (S)	1	14.784	882.184	<0.001
Alternative tactics (A)	1	0.385	22.964	<0.001
Population (P)	1	0.025	1.511	0.220
Error	277	0.017		

($P < 0.001$). Mass-specific somatic energy did not differ between alternative tactics in this population ($P = 0.25$).

Proximate composition in testes differed between alternative tactics in the Shikaribetsu population (for water, fat, and protein, all $P < 0.001$; Table 2), consistent with the pattern observed in soma except for similar proportions of ash ($P = 0.09$; cf. Tables 1 and 2). Mass-specific testicular energy was significantly lower in migrants ($P < 0.001$). In the Shumarinai population, proximate composition and mass-specific energy in testes were similar for alternative tactics (all $P > 0.17$).

Relative testicular investment

The slope of testicular energy on somatic energy did not differ between alternative tactics or populations (for all interaction terms in the full ANCOVA model, $P > 0.49$), nor did the slope of testicular mass on somatic mass (all $P > 0.69$). The final ANCOVA detected the significant effect of alternative tactics on testicular energy or mass (both $P < 0.001$, one-tailed; Table 3), together with the covariate effect of somatic energy or mass (both $P < 0.001$). In other words, testicular energy and mass were significantly higher in mature parr, independent of somatic investment (Fig. 2). The effect of population in the ANCOVA was significant for testicular energy ($P < 0.001$), but not for testicular mass ($P = 0.22$).

In terms of energy, mean GSI ± standard deviation (SD) of mature parr was 10.6 ± 2.6% and 13.1 ± 3.1% for the Shikaribetsu and Shumarinai populations, respectively (Fig. 3*a*). The corresponding value of migrants was 6.7 ± 1.6% and 6.4 ± 1.5% for the corresponding populations. Mean mass-based GSI ± SD was 13.0 ± 3.3% and 14.0 ± 3.3% for the Shikaribetsu and Shumarinai parr and 8.0 ± 1.9% and 6.7 ± 1.6% for the corresponding migrants, respectively (Fig. 3*b*).

Discussion

Mass-specific testicular energy ($kJ \cdot g^{-1}$) was lower in migrants than in mature parr in Shikaribetsu Lake but was similar for them in Shumarinai Reservoir. Such a discrepant result between populations was also found in mass-specific somatic energy, indicating that specific energy per tissue

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Fig. 2. Relative testicular investment. (*a*) Total testicular energy relative to total somatic energy and (*b*) testicular mass relative to somatic mass for mature parr (●) and migrants (■) in Shikaribetsu Lake and mature parr (○) and migrants (□) in Shumarinai Reservoir. The common slope is 0.933 for energy and 0.973 for mass.

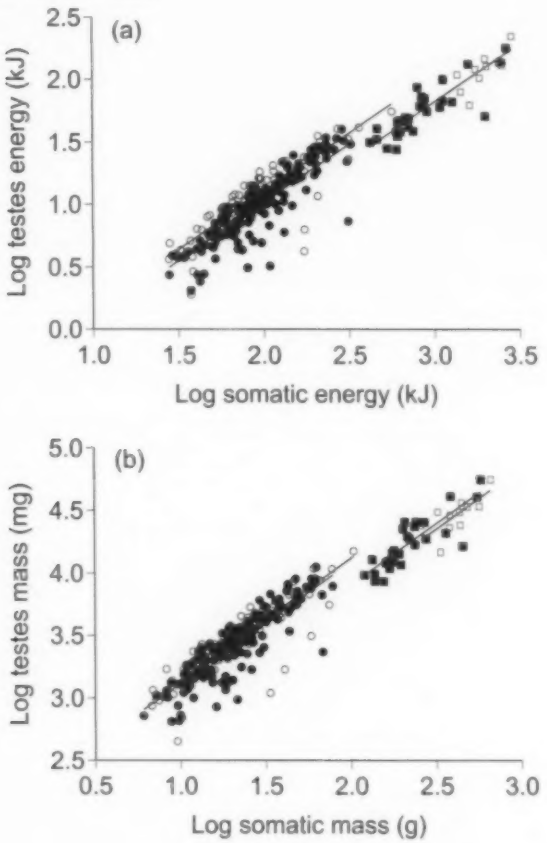
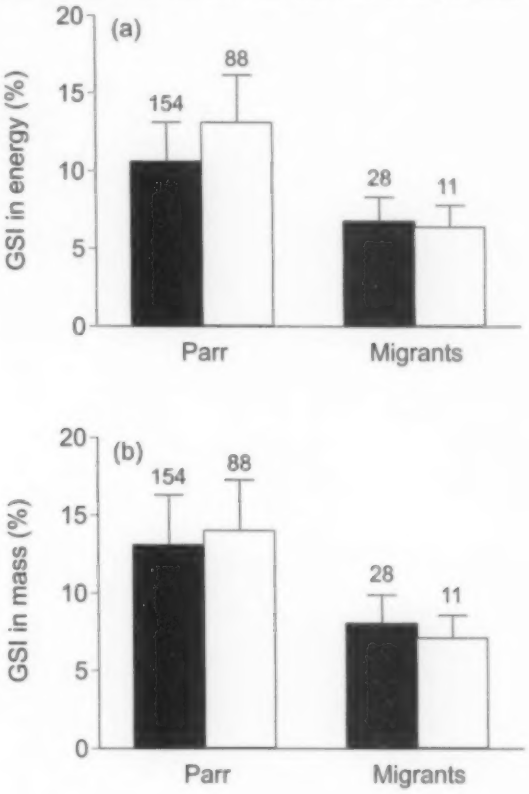


Fig. 3. Mean gonadosomatic index (GSI, the proportion of testes investment to the somatic investment) in terms of (*a*) total energy and (*b*) wet mass for mature parr and migrants in Shikaribetsu Lake (■) and Shumarinai Reservoir (□). Error bars denote standard deviations. Numbers above the bars refer to sample sizes.



mass poorly exhibits energy allocation pattern inherent in alternative tactics. Moreover, the monotonically decreased specific energy of testes and soma in the Shikaribetsu migrants suggests that specific energy is strongly influenced by external (or environmental) conditions of populations. One of the most likely environmental conditions is food availability. Feeding experiments in brown trout have demonstrated that ration size increases the proportions of fat and protein and hence mass-specific energy (Elliott 1976). Furthermore, Jonsson and Jonsson (1997) found in brown trout populations of Norway that migratory (anadromous) fish have a higher mass-specific somatic energy relative to resident fish, mainly because of a higher fat content. They attributed this difference to the higher food availability in the marine habitats (fjord and coastal sea). Our results in the Shikaribetsu population, where migrants had a lower mass-specific somatic energy resulting from a considerably lower fat content, can be considered to be opposite to the results from brown trout. Although the specific energy in tissues of anadromous masu salmon is currently unknown and has to be evaluated for strict intraspecific comparison, resource scarcity is a reasonable factor for the poor energy condition of the Shikaribetsu migrants.

Despite the complicated variance of mass-specific energy, total testicular energy (kJ) relative to total somatic energy showed that mature parr have a higher energy allocation to testes than migrants. We emphasize that our result is not affected by the difference of body size between alternative tactics. Some studies have identified that the allometric effect of body size on energy allocation is not isometric or that different-sized individuals allocate energy to a tissue and (or) function at different rates (Jonsson and Jonsson 1997; Post and Parkinson 2001). In this study, however, the log–log relationship between testicular energy and somatic energy (i.e., body size) is linear with no significant difference in slope between alternative tactics or populations. Therefore, the difference in total testicular energy between alternative tactics does not result from the difference in body size but in mating pattern per se.

Higher energy allocation to testes in mature parr supports our inference that the superior sperm characteristics adapted to sperm competition (Daye and Glebe 1984; Gage et al. 1995; Vladić and Järvi 2001) may require higher energy expenditure. Therefore, it is suggested that sperm competition is a responsible factor for the evolution of different testicular

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investments in alternative tactics. An increased testicular investment in mature parr may contribute not only to the greater sperm number per volume (Daye and Glebe 1984; Gage et al. 1995; Hoysak and Liley 2001), but also, in part, to the higher sperm ATP concentration (Vladić and Järvi 2001), which may in turn improve the sperm motility and fertilizing efficiency (Gage et al. 1995; Vladić and Järvi 2001; but see Hoysak and Liley 2001).

Consistent with the pattern observed in total energy, the testicular mass, relative to somatic mass, of mature parr was heavier than that of migrants. Moreover, both in terms of energy and mass, mean GSI of mature parr was 1.6 and 2.1 times as high as migrants for the Shikaribetsu and Shumarinai populations, respectively. Such a high consistency between the results in energy and mass provides not only a further support for our findings in energy, but also, at least in salmonids, a solid basis for the use of tissue mass as substitute of energy investment. In this context, information on mass-based GSI can be used to generalize energy allocation patterns of alternative tactics. Previous studies in Atlantic and sockeye salmon have reported approximately twofold higher mass-based GSIs for the mature parr and jacks, respectively (Gage et al. 1995; Foote et al. 1997). Taken together with our results in masu salmon, higher energy allocation to testes appears common among mature parr and jacks in salmonids.

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Reconstructing ecosystem dynamics in the central Pacific Ocean, 1952–1998. I. Estimating population biomass and recruitment of tunas and billfishes

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Abstract: Commercial yield of tunas in the central Pacific increased severalfold between 1952 and 1998. We developed age-structured production models that incorporate information from multiple fisheries to estimate population biomass and recruitment trends of tunas (*Thunnus alalunga*, *Thunnus albacares*, *Thunnus obesus*, and *Katsuwonus pelamis*) and billfish in the central north Pacific (0°N to 40°N and 130°E to 150°W). Our results suggest that all tuna stocks remain above 40% of 1950s levels, whereas blue marlin (*Makaira nigricans*) declined to 21% and swordfish (*Xiphias gladius*) to 56%. Estimated biomasses of juvenile bigeye (*T. obsesus*) and yellowfin (*T. albacares*) tuna increased to 112 and 129%, respectively, of 1950s levels. Juvenile albacore (*T. alalunga*) decreased during the 1970s and 1980s but recovered to historical highs (121%) in recent years. Skipjack (*K. pelamis*) remained relatively stable between 1952 and 1980, declined by 35% between 1981 and 1990, and then increased to 68% of 1950s levels. These changes generally represent decreases in top predators and increases in small tunas, which make up their prey. Application of stock assessment methods set in a food web context provides an important step toward developing a method that recognizes fishery exploitation as a component of ecosystem dynamics.

Résumé : Le rendement de la pêche commerciale au thon dans le centre du Pacifique s'est accru considérablement de 1952 à 1998. Nous avons mis au point des modèles de production structurés en fonction de l'âge qui incorporent les données provenant de nombreuses pêches commerciales dans le but d'estimer les tendances de la biomasse de la population et du recrutement des thons (*Thunnus alalunga*, *Thunnus albacares*, *Thunnus obesus*, et *Katsuwonus pelamis*), des espadons et des voiliers dans le centre-nord du Pacifique (0°N à 40°N et 130°E à 150°O). Nos résultats laissent croire que tous les stocks de thons sont demeurés au-dessus du seuil de 40 % des valeurs des années 1950, alors que le stock de makaires bleus (*Makaira nigricans*) a diminué jusqu'à 21 % et celui de l'espadon (*Xiphias gladius*), jusqu'à 56 %. Les biomasses estimées de jeunes thons ventrus (*T. obesus*) et d'albacores à nageoires jaunes (*T. albacares*) ont augmenté jusqu'à respectivement 112 et 129 % des valeurs des années 1950. Les jeunes germons (*T. alalunga*) ont décliné durant les années 1970 et 1980, pour récupérer et atteindre ces dernières années un niveau encore jamais enregistré de 121 %. Les stocks de thonines à ventre rayé sont restés relativement stables entre 1952 et 1980, pour décliner de 35 % entre 1981 et 1990 et ensuite remonter à 68 % des valeurs des années 1950. Ces changements représentent en général un déclin des grands prédateurs et une augmentation des petits thons qui constituent leurs proies. L'application de méthodes d'évaluation des stocks dans le contexte du réseau alimentaire représente une étape importante dans la mise au point d'une méthode qui reconnaisse l'exploitation par la pêche comme une composante de la dynamique de l'écosystème.

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Introduction

Single-species fisheries stock assessments are sometimes criticized for assuming that natural mortality or other population parameters (e.g., logistic model r, K) remain constant over time (Walters et al. 2000; Schnute and Richards 2001). Intuitively, these rates should vary in response to changes in the trophic structure of aquatic ecosystems and the habitats in which they are imbedded. There remains little doubt that human impacts caused by selective or incidental harvesting can significantly alter the trophic structure of food webs (Gislason et al. 2000; Jackson et al. 2001). Environmental forces can further influence trophic structure, the distribution of suitable habitat, and biological productivity that drives feeding and growth rates (Robinson and Ware 1999). Typically, however, the ultimate effects of such ecosystem changes on fish population dynamics and fisheries yields are difficult to identify because of a historical focus on single-species modeling and relatively imprecise, short time series of abundance and environmental data. Thus, the assumption of constant growth and mortality rates in fisheries stock assessments is, in part, borne out of a lack of understanding of the ways in which various forces contribute to variation in production.

In this paper (part I of II), we apply single-species stock assessment methods to estimate historical biomass and recruitment of tunas and billfishes in the central north Pacific Ocean (CNP), which we define as the epipelagic waters from 0°N to 40°N and from 130°E to 150°W. Assessments for many tuna species in the Pacific already exist as part of Secretariat of the Pacific Community (SPC) and Inter-American Tropical Tuna Commission (IATTC) research programs. SPC research efforts are mainly applied to western–central and south Pacific stocks, whereas IATTC efforts primarily focus on eastern tropical stocks. Furthermore, the stock assessment models used also differ between agencies and tend to cover different time periods. Therefore, we chose to develop our own assessments to provide a common modeling framework, historical reference period, and spatial coverage for the CNP proper as defined above. The assessment model we develop also has a similar structure to that used in our multispecies models (Cox et al. 2002), thus avoiding inconsistency between approaches that may simply be due to differences in structural details (i.e., age-based versus length-based assessments). We do, however, make extensive comparisons between our estimates of biomass and fishing mortality rates and those of SPC because there is generally substantial spatial overlap between their tuna assessments and those of the CNP.

Results presented here are then used (Cox et al. 2002) to calibrate a multifleet, whole-ecosystem model for assessing how estimated changes in trophic structure could influence natural mortality and production parameters of both predator and prey species. An area as large as the CNP has a high degree of spatial structure and multiple fisheries that target size- and age-structured populations. However, our goal is to integrate single-species and ecosystem approaches to extract general patterns and relationships between fisheries and trophic interactions. Such integration is critically needed if ecosystem modeling approaches are to become an additional tool for evaluating management options.

Methods

Central Pacific fisheries data

Pelagic fisheries in the Pacific are typically segregated into deepwater longline fleets that target large-sized bigeye (*Thunnus obesus*), yellowfin (*Thunnus albacares*), and albacore (*Thunnus alalunga*) tuna and surface fleets that target all ages and sizes of skipjack tuna (*Katsuwonus pelamis*), small-sized bigeye and albacore, and all ages and sizes of yellowfin. Surface fleets include purse-seine, large-mesh gillnet (i.e., driftnet), small-mesh gillnet, handline, ringnet, pole-and-line, and troll. Annual catch and fishing effort (except troll) for each gear type were obtained from the Secretariat of the Pacific Community, Ocean Fisheries Programme catch–effort database for the region (SPC 2000) and the tuna fishery yearbook (Lawson 2000). All catch data were scaled to units of density ($kg \cdot km^{-2}$) by dividing total catches by 30×10^6 km^2, which is the total area of the CNP.

We used fishing effort estimates from logbook data for purse-seine, longline, pole-and-line, and other gears because this effort was available specifically for the CNP area (SPC 2000). Longline fishing effort for the bigeye tuna assessment was adjusted to reflect effective fishing effort targeting bigeye (Bigelow et al. 1999). Effort by the troll fleet was calculated by dividing total troll catch by aggregate catch per unit fishing effort (CPUE) indices from all countries (Shaw and Bartoo 1997). Effort data were scaled to the mean effort between 1990 and 1998. For the driftnet fishery that occurred between 1979 and 1992, we used relative total catch (Bartoo et al. 1997) as a surrogate for effort because we were unable to locate an appropriate effort index.

Assessment model

Analyses of population and recruitment trends were performed using a combined age-structured – delay-difference model. We used an age-structured formulation for immature stages to account for recruitment variation and removals by surface fisheries, which primarily target younger age-classes. A Deriso–Schnute delay-difference formulation (Deriso 1980; Schnute 1985) then accounted for biomass dynamics and harvest of fully mature fish in deepwater fisheries. We assumed that recruitment to the reproductive adult stage occurs at age k. Although age-at-maturity is not necessary in this model (i.e., we use no stock–recruitment relationship), we apply it here so that our estimates of juvenile and adult biomass dynamics from single-species models will be comparable to those obtained from multispecies models (Cox et al. 2002) that attempt to predict compensatory recruitment processes. The catch equations and stock dynamics for the current models are given by (see Table 1 for notation)

$$(1)\quad C_{a,j,t} = \frac{F_{a,j,t}}{Z_{a,t}}[1 - \exp(-Z_{a,t})]B_{a,t}$$

$$(2)\quad B_{1,t} = Rm_1 \exp(w_t)$$

$$(3)\quad B_{a,t} = N_{a-1,t-1}m_a \exp(-Z_{a-1,t-1}), \quad 2 \le a \le k-1$$

$$(4)\quad B_{k,t} = \exp(-Z_{k,t-1})(\alpha N_{k,t-1} + \rho B_{k,t-1}) + N_{k-1,t-1}m_k \exp(-Z_{k-1,t-1})$$

$$(5)\quad F_{a,j,t} = q_j E_{j,t} s_{a,j}$$

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Table 1. Notation and symbols for central Pacific fisheries models.

Symbol	Description
Indexes	
t	Subscript for year (t = 1, 2,...,T)
a	Subscript for age
j	Subscript for fishing gear (j = 1, 2,...,J)
Estimated parameters	
R	Mean recruitment of age-1 fish (individual fish·km^{-2})
w_t	Recruitment anomaly in year t
q_j	Catchability coefficient for gear j
ε_t	Effort deviation in year t
Fixed parameters	
α	Intercept of the Ford–Brody growth equation (kg)
ρ	Slope of the Ford–Brody growth equation (kg·year^{-1})
k	Age-at-recruitment to adult stock (year)
$s_{a,j}$	Selectivity of age a fish by gear j
m_a	Body-mass-at-age a (kg) from recursion $m_a = \alpha + \rho m_{a-1}$
m_k	Body-mass-at-recruitment to adult stock (kg)
M_{ad}	Instantaneous natural mortality rate for adults (year^{-1})
M_j	Instantaneous natural mortality rate for juveniles (year^{-1})
Unobserved states	
$C_{a,j,t}$	Predicted catch (kg·km^{-2}) at age a by gear j at time t
$F_{a,j,t}$	Fishing mortality rate imposed on age a fish by gear j in year t (year^{-1})
$Z_{a,t}$	Total mortality rate for age a fish in year t (year^{-1})
$B_{a,t}$	Predicted biomass (kg·km^{-2}) of age a fish in year t
$N_{a,t}$	Predicted numbers of age a fish in year t (individual fish·km^{-2})
$\hat{Y}_{j,t}$	Predicted CPUE by gear j in year t
$\overline{m}_k$	Equilibrium mean body mass for oldest age-class (k)
Observed states	
$E_{j,t}$	Fishing effort by gear j in year t
$Y_{j,t}$	Observed CPUE-by-gear j in year t

Note: CPUE = catch-per-unit-effort.

$$(6) \qquad Z_{a,t} = M_a + \sum_j F_{a,j,t}$$

The assessment model subdivides the biomass dynamics of a given species into three components: (*i*) age-class 1 recruits (eq. 2) for which we assume all births take place at the beginning of the year before fishing; (*ii*) an age-structured component for ages 2 to $k - 1$ (eq. 3); and (*iii*) a plus-group component in which fully mature fish (all ages $\geq k$) are lumped into age-class k (eq. 4). For this oldest age-class, we used a delay-difference equation to account for growth and mortality. For tunas, growth parameters α and ρ were obtained from reviews on the biology of each species (FAO 1994). Natural mortality rates, assumed constant for juveniles and for adults, were obtained from tagging studies (Hampton 2000; Table 2). Growth data for blue marlin (*Makaira nigricans*) and swordfish (*Xiphias gladius*) were obtained from Skillman and Young (1976) and Sakagawa and Bell (1980), respectively.

Initial distributions of numbers- and biomass-at-age were calculated by assuming that these were at equilibrium with respect to fishing mortality rates during the early 1950s. Thus, numbers-at-age for the first model year were

$$(7a) \qquad N_{1,1} = R$$

$$(7b) \qquad N_{a,1} = N_{a-1,1} \exp(-Z_{a-1,1}), \quad 2 \leq a \leq k - 1$$

Table 2. Growth and mortality parameters used for assessment models.

Group	k	m_k	α	ρ	M_j	M_{ad}
Bigeye	4	39.0	16.6	0.93	0.6	0.3
Yellowfin	2	14.8	41.5	0.75	1.5	0.8
Albacore	5	13.3	5.1	0.91	0.2	0.3
Skipjack	2	13.4	13.4	0.70	1.9	1.9
Blue marlin	5	44.0	27.0	0.95	0.4	0.2
Swordfish	2	10.0	23.6	0.79	0.4	0.2

Note: Variables defined in Table 1. Natural mortality rates for juvenile blue marlin and swordfish are for age-1 fish only.

$$(7c) \qquad N_{k,1} = \exp(Z_{k-1,1}) N_{k-1,1} / (1 - \exp(-Z_{k,1}))$$

Initial biomass-at-age was obtained by multiplying numbers-at-age by mean body-mass-at-age for all ages $\leq k - 1$. For the oldest age-class k, we used the equilibrium mean body mass equation

$$(8) \qquad \overline{m}_k = \frac{[\exp(-Z_{k,1})\alpha + m_k(1 - \exp(-Z_{k,1}))]}{[1 - \rho \exp(-Z_{k,1})]}$$

Initial adult biomass $B_{k,1}$ was then obtained by multiplying mean adult body mass (eq. 8) by total numbers in the adult

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age-class (eq. 7*c*). Note that equilibrium adult body mass is only used to initialize the model in the first year. Mean adult body mass in later years may be calculated by dividing total adult biomass $B_{k,t}$ by total adult numbers $N_{k,t}$.

Because our catch data were aggregated over age-classes, we used a rather crude representation of selectivities-at-age for different fleets $s_{a,j}$. Selectivities for ages $a \leq k - 1$ were assigned values of 1 for surface gear and 0 for longline gear. Selectivity for adults ($a = k$) was 0 for surface gear and 1 for longline gear. We made two exceptions to this selectivity scheme: (*i*) for juvenile albacore we used values of 0.50, 0.75, 1.0, and 1.0, for ages 1 through 4, respectively, in surface fisheries and 0 for longline because selectivity estimates were available for the south Pacific stock (Fournier et al. 1998); and (*ii*) for adult yellowfin, we used selectivity of 1 for purse-seine fisheries because catches of sets on free-swimming schools are dominated by large yellowfin.

For each year, predicted total catch for a given gear type was obtained by taking the sum of catches $C_{a,j,t}$ over all age groups. Predicted CPUE $\hat{Y}_{j,t}$ was then calculated by dividing gear-specific predicted catches by observed gear-specific fishing effort.

Parameter estimation

Parameters to be estimated for each species included the mean recruitment level R, a vector of annual recruitment anomalies $\mathbf{w}$, and a catchability vector $\mathbf{q}$ giving a total of $T + J + 1$ parameters. For the CPUE-by-gear data, we used the observation model

$$(9) \qquad Y_{j,t} = \hat{Y}_{j,t} e^{u_{j,t}}$$

where the $u_{j,t}$ are assumed to be independent, normal observation errors with mean zero and variance $\sigma^2_{u,j}$. Therefore, the negative log-likelihood for the CPUE observations L_1 is

$$(10) \qquad L_1 = \sum_j \lambda_j \sum_t (\ln Y_{j,t} - \ln \hat{Y}_{j,t})^2$$

where the weight factor λ_j is the squared inverse of the assumed coefficient of variation for gear type j observations. We used weight factors $\lambda_j = 25$, which are equivalent to coefficients of variation of 0.2.

The following negative log-likelihood component assumes that the recruitment anomalies are independent and normally distributed:

$$(11) \qquad L_2 = \lambda_R \mathbf{w}^T \mathbf{w}$$

The weight factor $\lambda_R = 2.5$ assumes that the coefficient of variation of the recruitment anomalies is approximately 0.6 (T in eq. 11 indicates the transpose operation). A stronger constraint was used for swordfish ($\lambda_R = 25$) because the recruitment estimates were particularly sensitive to increases in CPUE during the late 1980s when the Hawaii-based longline fishery targeting swordfish developed.

For all species, we included a normal prior on the logarithm of 1990–1998 average adult fishing mortality to constrain the upper limit on biomasses. In all cases, a noninformative prior with mean $F = 0.1$ year^{-1} and a coefficient of variation of approximately 31 ($\lambda_F = 0.001$) was sufficient and did not influence the results substantially (i.e., using a prior $F = 0.3$ year^{-1} did not change overall mean fishing mortality or biomass estimates).

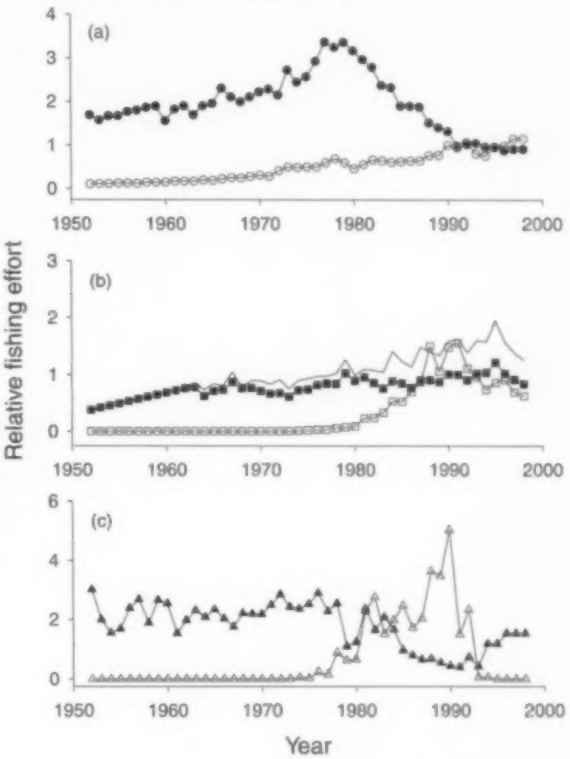

Fig. 1. Relative fishing effort (1952–1998) for the six major fishing fleets operating in the central Pacific Ocean. All values are scaled to the 1990 to 1998 mean effort. (*a*) Pole-and-line (solid circles) and other gear (open circles); (*b*) nominal longline (solid squares), effective bigeye longline (solid line), and purse-seine (open squares); (*c*) troll (solid triangles) and driftnet (open triangles).

Most CNP species in this analysis are captured by three to five gear types. Thus, for each population, we had several indices of abundance that could be used to estimate model parameters. Preliminary analyses indicated that some of the gear-specific, observed catches could not be explained by changes in fishing effort or recruitment. Where such discrepancies occurred, we attributed this lack of fit to deviations from the deterministic fishing effort – fishing mortality relationship (Fournier et al. 1998) for a particular gear type, and we accounted for it in the model by introducing an additional vector of normally distributed $(0, \sigma^2_\varepsilon)$ effort deviation parameters. These parameters were used for only one gear type per species to eliminate confounding of effort deviations among gear types. Incorporating effort deviations for a particular gear type was done by computing annual fishing mortality as

$$(12) \qquad F_{a,j,t} = q_j E_{j,t} s_{a,j} \exp(\varepsilon_t)$$

The contribution of effort deviations to the total negative log-likelihood is of the form

$$(13) \qquad L_3 = \lambda_3 \varepsilon^T \varepsilon$$

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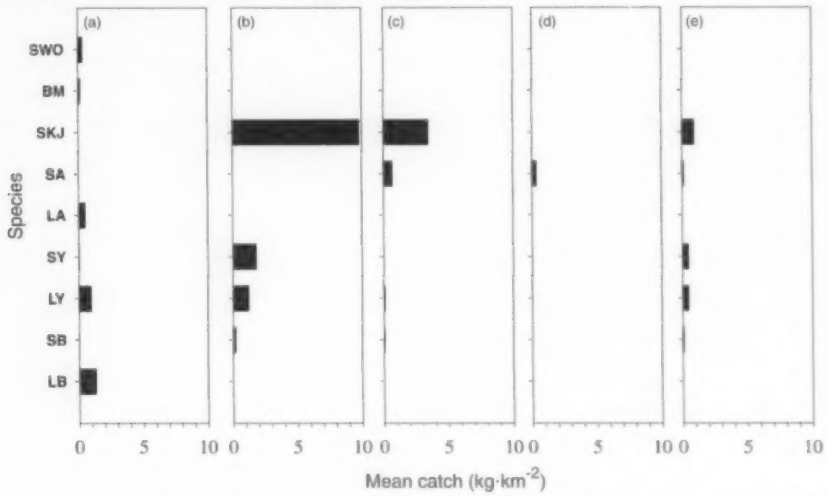
Fig. 2. Mean total catch (1990–1998) in central Pacific tuna-directed fisheries: (*a*) longline; (*b*) purse-seine; (*c*) pole-and-line; (*d*) driftnet; (*e*) other gear. Species codes: SWO, swordfish (*Xiphias gladius*); BM, blue marlin (*Makaira nigricans*); SKJ, skipjack (*Katsuwonus pelamis*); SA, small albacore (*Thunnus alalunga*); LA, large albacore; SY, small yellowfin (*Thunnus albacares*); LY, large yellowfin; SB, small bigeye (*Thunnus obesus*); and LB, large bigeye.



where the weight factor $\lambda_3 = 25$ is equivalent to a coefficient of variation of 0.2 around the mean fishing effort – fishing mortality relationship. The choice of whether or not to use effort deviation parameters to improve the fit, or to which gear type they should apply, was determined using the log-likelihood ratio test (Hilborn and Mangel 1997):

$$\mathcal{R}_{jk} = 2[L_j(\theta_j) - L_k(\theta_k)]$$

where $\mathcal{R}_{jk}$ is the log-likelihood ratio of model j with parameters θ_j over model k with parameters θ_k. The test statistic $\mathcal{R}$ is distributed as χ^2 with $n_j - n_k$ degrees of freedom. Alternative models are referred to as either null (no deviations applied) or by the specific gear to which they are applied. We used the estimated mean fishing mortality between 1990 and 1998 on juveniles and adults as a check on the sensitivity of the results to these alternative models.

The model was implemented in AD Model Builder version 6.0.3 (Otter Research Ltd. 2000). Parameter estimates were obtained by minimizing the sum of eqs. 10, 11, and 13 with respect to parameters R, $\mathbf{w}$, $\mathbf{q}$, and $\boldsymbol{\epsilon}$.

Results and discussion

Historical changes in the CNP fishery

Longline, troll, and pole-and-line fleets all operated within the CNP during the early 1950s; therefore, for most species, 1950s biomass estimates given below do not represent unfished conditions. Pole-and-line fishing effort approximately doubled between 1952 and 1980 but then decreased to present levels, whereas fishing effort by other gear types (mainly small-mesh gillnet) has been increasing throughout the 1952–1998 time period at a rate of approximately 5% per year (Fig. 1*a*). Nominal longline effort and effective longline effort for bigeye increased continuously; however, effective effort for bigeye increased relative to nominal effort after 1980 (Fig. 1*b*). Purse-seine fisheries were relatively unimportant until large-scale development began in the late 1970s and early 1980s, after which effort increased rapidly reaching a peak in the early 1990s (Fig. 1*b*). Troll fishing effort, which mainly targets albacore, showed little trend until a strong decline began in the early 1980s (Fig. 1*c*). The decline and subsequent reversal of troll fishing effort was coincident with development and ultimate closure of the high-seas driftnet fishery that operated between the late 1970s and early 1990s (Fig. 1*c*).

Yield of skipjack and yellowfin constitutes over 70% of the current total tuna and billfish landings from the CNP. Skipjack dominated commercial catches over the entire 1952–1998 time period, and current skipjack yields from purse-seine and pole-and-line fisheries make up over 60% of total tuna and billfish biomass harvested (Fig. 2). Although small yellowfin tuna harvest was negligible before full-scale purse-seine fishing in the 1980s, landings currently make up approximately 13% of total yield. The proportions of total yield accounted for by large bigeye, large yellowfin, and large and small albacore have declined since the 1960s and currently range from 2 to 8%. However, this mainly reflects the increasing domination by small tunas because absolute yields of these species have actually increased. Blue marlin and swordfish were not targeted by longlines for most of the time series; however, they both have significant commercial value as bycatch species. Swordfish were targeted by longlines during the 1950s and early 1960s, but interest then shifted toward tunas. Swordfish effort increased in the late 1980s as the fleet grew rapidly when mainland-based boats moved to Honolulu and targeted the region north and east of Hawaii. That fishery is now strongly influenced by conservation concerns associated with bycatch of sea turtles. Blue marlin and swordfish currently make up only 0.1 and 1% of total landings, respectively.

Model fitting

Likelihood ratio tests indicated that effort deviation pa-

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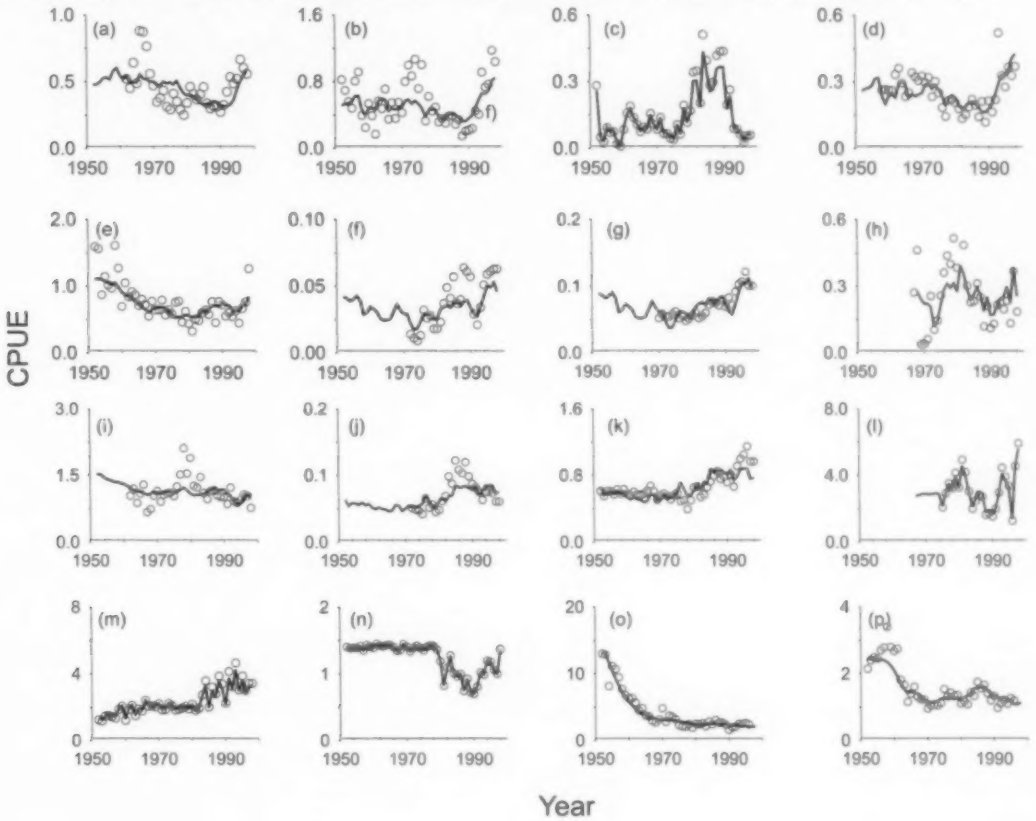
Fig. 3. Observed (circles) and predicted (lines) catch-per-unit effort (CPUE) of tunas and billfish in the central Pacific: (*a*) albacore (*Thunnus alalunga*), longline; (*b*) albacore, pole-and-line; (*c*) albacore, other gear; (*d*) albacore, troll (driftnet albacore not shown); (*e*) bigeye (*Thunnus obsesus*), longline; (*f*) bigeye, pole-and-line; (*g*) bigeye, other gear; (*h*) bigeye, purse-seine; (*i*) yellowfin (*Thunnus albacares*), longline; (*j*) yellowfin, pole-and-line; (*k*) yellowfin, other gear; (*l*) yellowfin, purse-seine; (*m*) skipjack (*Katsuwonus pelamis*), pole-and-line; (*n*) skipjack, other gear; (*o*) blue marlin (*Makaira nigricans*), longline; (*p*) swordfish (*Xiphias gladius*), longline.



rameters significantly improved the overall fit of all tuna models. For albacore, effort deviations were applied to other gear fisheries because CPUE (Fig. 3*c*) showed a completely opposite temporal pattern compared with CPUE from the other three gear types (Figs. 3*a*, 3*b*, 3*d*). The observed pattern is probably due to misreporting of albacore driftnet catches as coming from other gear because the temporal patterns of catches from other gears and driftnet were nearly identical. Although the effort deviation parameters accounted for higher observed catches, the estimated mean fishing mortality rate during the 1990s did not change substantially for both immature and adult fish (Table 3).

Effort deviations were applied to purse-seine effort for bigeye tuna (Fig. 3); however, mean 1990s fishing mortality was similar for all models considered (Table 3). The adult fishing mortality rate estimate for this model F_{1990s} = 0.18 year^{-1} is similar to estimates based on tagging data from the tropical Pacific (Hampton 2000) and a Pacific-wide length-based assessment (Hampton and Fournier 2001*a*). Our estimate of fishing mortality for juvenile bigeye F_{1990s} = 0.09 year^{-1} is well below 0.50 year^{-1}, which was the (approximate) average fishing mortality for 21- to 100-cm bigeye reported by Hampton (2000) but is nearly identical to that estimate for age-classes 1–4 in the Pacific-wide assessment (Hampton and Fournier 2001*a*).

Surface gear CPUE indices for yellowfin were similar to those of bigeye with two showing increasing trends and one indicating a decline and recovery in the 1980s and 1990s (Figs. 3*i*–3*l*). Initial estimates based on the null model showed a two- to three-fold difference between predicted and observed purse-seine catches during the early 1990s. Accounting for these differences significantly improved the model fit and resulted in higher estimated fishing mortality over the null model (Table 3). Final estimates of fishing mortality for small yellowfin (age-class 1) were lower than those estimated for 31- to 40-cm fish from tagging (Hampton 2000; F = 0.80 year^{-1}) but were similar to estimates from a spatially explicit, length-based model assessment (Hampton and Fournier 2001*b*), which were generally around 0.50 year^{-1}. The estimate for adults is greater than both of the above studies, which probably reflects our assumption that large yellowfin are fully vulnerable to purse-seine fisheries. Despite the differences in the absolute value of fishing mortality (i.e., scale of biomass estimates), the estimated trends in recruitment that

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Table 3. Results of likelihood ratio tests for alternative fishing mortality models.

Species and model	Log-likelihood	No. parameters	P	F_j	F_{ad}
Albacore					
Null	2963	53		0.16	0.04
Other gear	**2255**	100	<0.01	0.15	0.06
Pole-and-line	2649	100	<0.01	0.08	0.01
Bigeye					
Null	393	53		0.10	0.17
Pole-and-line	336	100	<0.01	0.11	0.17
Purse-seine	**305**	81	<0.01	0.09	0.18
Other gear	375	100	>0.05	0.11	0.17
Yellowfin					
Null	187	52		0.49	0.24
Purse-seine	**106**	75	<0.01	0.51	0.25
Pole-and-line	139	74	<0.01	0.41	0.19
Skipjack					
Null	197	51		—	<0.01
Pole-and-line	**51**	98	<0.01	—	1.12
Other gear	71	98	<0.01	—	<0.01

Note: Null denotes fully deterministic models in which no effort deviations were used. Alternative models are denoted by the gear type to which effort deviations are applied. Best-fitting models are indicated by boldfaced log-likelihood values. Probability levels (P) are based on the χ^2 distribution with degrees of freedom equal to the difference in numbers of parameters between the null and the alternatives. Model sensitivity is represented by alternative estimated mean 1990s fishing mortality for juveniles F_j (F averaged over all immature age-classes $a \leq k - 1$) and adults F_{ad}.

we show below were nearly identical for all of the models considered. They were also similar to those estimated by Hampton and Fournier (2001*b*).

Of the three gears that target skipjack, only pole-and-line CPUE showed an increase during the past two decades (Fig. 3*m*). Purse-seine CPUE was nearly identical to other gear over the period 1975–1998 (Fig. 3*n*; other gear). Of particular interest in this case is that increases in pole-and-line CPUE coincided with a large-scale effort reduction for this fleet as less competitive boats were removed from the fishery with some converted to purse-seine vessels (FAO 1994; Lewis and Williams 1999). The implied increase in mean catchability for the remaining vessels in the fleet was supported by preliminary assessments for the southern portion (15°N to 20°S and 120°E to 150°W) of this stock (Hampton et al. 2000). The addition of effort deviation parameters to account for these changes significantly improved the overall model fit but also caused a large increase in the estimated fishing mortality rate during the 1990s compared with the null and other gear models. For the pole-and-line model, 1990s fishing mortality was 1.12 year^{-1}, whereas fishing rates for the null and other gear models were both less than 0.01 year^{-1} (Table 3). Although this indicates high sensitivity to effort deviation parameters, the fishing mortality rate estimate for the pole-and-line model is similar to that suggested in the preliminary assessment for the southern portion of this stock and published estimates based on tagging data by Hampton 2000.

Although blue marlin and swordfish are taken in small quantities as bycatch in tuna-directed surface fisheries (Lawson 2000), time series of catches were only available from longline fisheries. The blue marlin longline CPUE data suggested a strong decline in response to increasing fishing effort as estimated fishing mortality increased from 0.06 year^{-1} in the 1970s to 0.26 year^{-1} at present (Fig. 3*o*). Although swordfish CPUE in the longline fishery also showed an early decline, total depletion did not appear as large and CPUE has remained relatively stable since the 1970 (Fig. 3*p*). Estimated current fishing mortality for swordfish is approximately 0.25 year^{-1}. For both species, CPUE may be influenced by changes in tuna targeting practices, and this is not accounted for in our estimates (see below).

Population biomass trends

Albacore

The dynamics of albacore have been studied intensively (Anonymous 2001), and most findings agree on the pattern of decline during the 1980s and subsequent increase during recent years (Fig. 4*a*). Estimated biomass of juvenile albacore began to decline during the late 1970s, continued declining into the mid-1980s, and then increased rapidly with present levels approximately 1.5 times the 1952–1990 average (Fig. 4*b*). The initial declining phase appears to have been caused in part by increasing fishing mortality rates on age-1 to age-4 small albacore that reached a peak of approximately 0.25 year^{-1} around 1980. This fishing mortality rate is close to the natural mortality rate $M = 0.20$ year^{-1} that we used for small albacore and thus has a significant effect on the estimated rate of decline. Recruitment anomaly estimates (Fig. 5*a*) suggest that age-class 1 recruitment was below average from 1983 to 1990 compared with total immature biomass, which remained below average between 1976 (i.e., start of high-seas driftnet fishing) and 1991.

Our estimates of north Pacific albacore recruitment are of similar magnitude to those reported for the south Pacific stock based on a more complicated length- and sex-based model formulation and detailed data (Fournier et al. 1998;

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Fig. 4. Biomass estimates (thick line) and 95% confidence limits (thin lines) for tunas and billfishes in the central Pacific: (*a*) large albacore (*Thunnus alalunga*); (*b*) small albacore; (*c*) skipjack (*Katsuwonus pelamis*), all sizes; (*d*) large bigeye (*Thunnus obsesus*); (*e*) small bigeye; (*f*) blue marlin (*Makaira nigricans*), all sizes; (*g*) large yellowfin (*Thunnus albacares*); (*h*) small yellowfin; (*i*) swordfish (*Xiphias gladius*), all sizes.

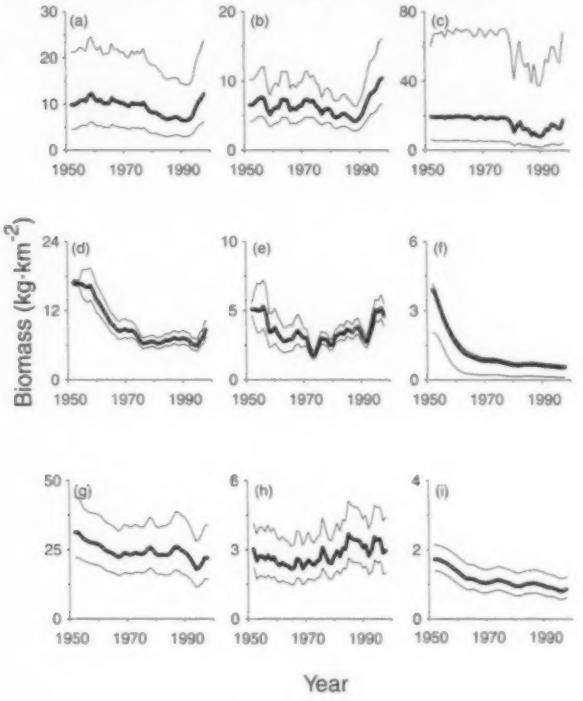

Fig. 5. Estimated numbers of age-class 1 albacore tuna (*Thunnus alalunga*) in the central Pacific: (*a*) north Pacific albacore (solid line) and south Pacific albacore (broken line; from Fournier et al. 1998); (*b*) phase plot of albacore recruitment versus adult albacore biomass (years before 1970 are not shown to reduce clutter).

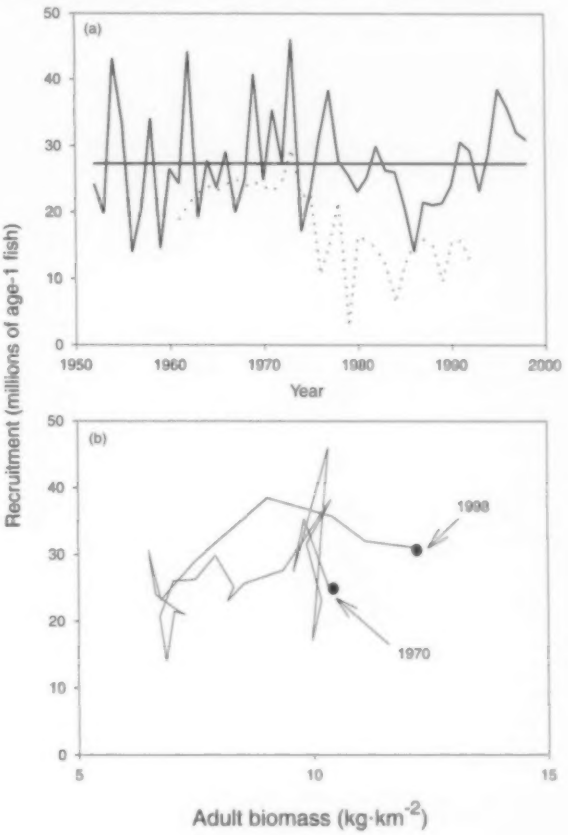

Fig. 5*a*). However, in the south Pacific case, age-1 albacore abundance showed a strong decline during the 1970s, which the authors suggested was correlated to the Southern Oscillation Index (SOI; Fournier et al. 1998). Our estimates of north Pacific albacore recruitment were not correlated to those of the south Pacific ($r = 0.30$, $P > 0.05$) or to the SOI ($r = 0.12$, $P > 0.05$). Rather, the dynamics that we observed for albacore suggest that high fishing mortality on small albacore resulted in a decline in biomass of adults, which then caused a further decline in recruitment. Higher survival of small albacore following closure of high-seas driftnet fishing then appears to have caused increases in both adults and age-class 1 recruits (Fig. 5*b*).

Skipjack

Although skipjack are the most intensively fished species in the CNP, biomass appears to have remained relatively stable over most of the 1952–1998 time period. During the peak activity of the purse-seine fishery, total fishing mortality rate estimates exceeded 1.3 year^{-1} for several years, and this coincides with an approximate 35% decline in abundance during the 1980s (Fig. 4*c*). Adult and juvenile biomass trends were nearly identical mainly because we assumed that all fisheries equally select all ages. Therefore, we only show changes in total biomass. Interannual variability in total biomass is not well defined during the early years of the fishery because of the stability of pole-and-line and other gear CPUE indices. As the purse-seine fishery increased in importance and later dominated the catches, interannual variability in abundance increased. Although the earlier recruitments were stable, they did indicate a slight increasing trend until the purse-seine fishery developed. Pole-and-line and other gear fisheries were obtaining substantial yields of skipjack before purse-seine development and peak purse-seine catches more than doubled the already high harvest. The increase in catch raised estimated fishing mortality from approximately 0.3 year^{-1} during the early 1970s to over 1.3 year^{-1}. Total mortality was therefore greater than 3.0 year^{-1} during the peak purse-seining period and this caused a high within-year dependence between estimated abundance and recruitment ($r = 0.97$). This is understandable given that when annual survival is only 0.06, then within-year abundance becomes highly dependent upon recruitment. The purse-seine CPUE decline that followed was also supported by other gear CPUE, which indicated a similar decline so that the general pattern of decline and recovery seems plausible.

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The limited response to increasing exploitation means that most of the CPUE data are relatively uninformative, thus leading to a high degree of uncertainty in the biomass estimates as shown by the confidence limits in Fig. 4*c*. The general pattern of decline and recovery is similar to that estimated by the length-based assessment of Hampton et al. (2000).

Bigeye

Biomass of large bigeye tuna showed a relatively strong initial decline between 1952 and 1975 (Fig. 4*d*). Although fishing mortality increased steadily since then, biomass estimates remained stable over the past three decades. During this time, longline fisheries have increasingly developed better longline setting practices for targeting bigeye tuna (Bigelow et al. 1999). When not accounted for, such changes mask declines in abundance as indexed by CPUE because catchability would be increasing. Bigelow et al. (1999) adjusted fishing effort and CPUE indices based upon hooked depth and habitat preferences of bigeye and showed that CPUE appeared to decline further in the western and central Pacific than indicated by nominal CPUE indices. Our bigeye assessment incorporated these changes in effective fishing effort because the main area that we consider has had rather large changes in catchability over time. Thus, the biomass trends that we report are similar to SPC assessments (Hampton and Fournier 2001*a*).

Estimated small bigeye biomass declined initially but then increased since the 1970s (Fig. 4*e*). This pattern mainly reflects increasing pole-and-line and other gear CPUE. The initial decline in age-1 bigeye preceded the decline of adults, suggesting that some other factors besides adult stock were driving recruitment (Fig. 6). Estimates of bigeye recruitment from Hampton and Fournier (2001*a*; their region 1) also suggest increases since 1970; however, those did not appear to be as large.

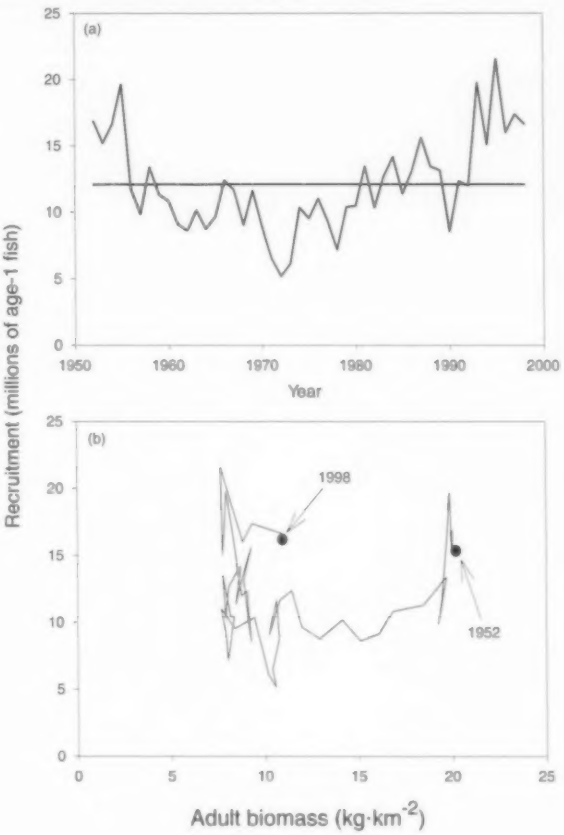
Yellowfin

Adult yellowfin biomass estimates indicated an initial decline followed by relative stability over the past several decades, despite increasing fishing mortality in longline and purse-seine fisheries and high fishing mortality on juveniles in purse-seine fisheries beginning in the 1980s (Fig. 4*g*). Adult biomass then declined sharply during the early 1990s but showed a recovery in recent years. Biomass of juveniles appears to have increased between 1970 and the mid-1980s and then remains relatively constant (Fig. 4*h*). This increase was somewhat suspicious given that it coincides with the development of purse-seine fisheries that catch more than four times that of the pole-and-line and other gear fisheries combined. However, despite such a large change in total harvest, pole-and-line and other gear CPUE data continued to indicate increases in juvenile production. The estimated trends in both adult and juvenile yellowfin are very similar to those estimated by Hampton and Fournier (2001*b*), despite the differences in fishing mortality rates mentioned above.

Billfish

Biomass estimates for blue marlin and swordfish both decline rapidly following early exploitation by longline fleets. Blue marlin (Fig. 4*f*) in particular showed apparently strong depletion, whereas swordfish (Fig. 4*i*) remained relatively stable throughout the 1960–1998 time period. Estimated declines in biomass for both of these species might be somewhat overestimated because of the changes in longline targeting (Hinton and Nakano 1996). Both species tend to be captured at shallower depths than the primary longline target species, which is bigeye. Thus, changes in fishing practices that increase effective effort for bigeye would decrease effective effort for these species. However, the rate of CPUE decline during the early years of exploitation may reflect actual declines for blue marlin in particular, because the major decline occurred well before longline setting practices changed during the 1970s.

Fig. 6. (*a*) Estimated numbers of age-class 1 bigeye tuna (*Thunnus obesus*) in the central Pacific. (*b*) Phase plot of bigeye tuna recruitment versus adult bigeye biomass.



Our analysis of tuna and billfish dynamics in the CNP appears to be relatively robust with respect to general time trends. Alternative parameterizations did not substantially change patterns of biomass response to increasing (or decreasing) fishing effort. Further, most of our fishing mortality estimates are similar to those estimated from tagging and modeling studies for several of these species in the western and central Pacific.

Limitations of central Pacific assessments

As with any stock assessment approach, our analyses of biomass dynamics of tunas and billfishes in the CNP area depend upon many layers of assumptions. Here we identify

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several of these and how they may impact our conclusions. First, although the CNP area as we have defined supports substantial catches, it is not the permanent habitat of any of the above species. Individual yellowfin tuna have been shown to range over all regions of the Pacific (Suzuki 1994), and those present in the CNP may spend considerable time in areas south of the equator (which we ignore). Bigeye tuna are found throughout the tropical Pacific without any clear evidence that discrete stocks exist (Miyabe 1994). Blue marlin tagged in sport fisheries off Hawaii have been recaptured as far as Fiji. Thus, the populations that we consider are likely also affected by fishing patterns and biophysical forces outside our model area. Comparisons between our results and those for larger areas of the western–central and south Pacific, however, suggest that we have captured the general patterns of changes in most CNP tuna and billfish stocks.

It is a well-known fact that fishery-dependent statistics such as CPUE are generally misleading as indices of abundance. Our assessments of CNP fisheries are no different. Catchability has likely changed over the past five decades because of improvements in vessel power, capacity, and technology, as well as increases in the effective area fished. Such issues pervade fisheries stock assessment and are not specific to our treatment of CNP fisheries. Most accepted assessments for Pacific tunas also rely on similar tenuous assumptions about CPUE data, but more detailed separation of fisheries, size structure of catches, and tag–recapture data provide at least some capability to address these assumptions. For example, SPC assessments routinely attempt to estimate long-term trends in catchability (Hampton and Fournier 2001*b*). Their analyses for yellowfin, for instance, show rather rapid increases in catchability (after 1995) for what we consider here as "other" gear. This had important implications for our recruitment estimates during this time. However, notice that our model ignored "other" gear CPUE increases over the same period, which suggests that we have detected poor correspondence between CPUE and abundance as well (Fig. 3*k*). Although our assessments may differ in the quantitative details, the general patterns of recruitment variation in the CNP are thus consistent among various approaches.

Declines of longline CPUE during the early period of development in the 1950s and 1960s for species such as blue marlin, swordfish, bigeye, and possibly yellowfin (Suzuki 1994) remain a subject of debate. The 1950s in particular was a period in which Japanese boats dominated the fishery and their activity was concentrated in the northwest Pacific. Therefore, CPUE declines may reflect localized fishing impacts that do not represent changes in the CNP stock as a whole. The 1960s was a period of rapid spatial expansion as longline fisheries extended activity to all areas of the Pacific. Yet catch rates of blue marlin and bigeye in particular continued to decline. This pattern is just the opposite of that which is expected from catch rates of an expanding fishery: CPUE should remain high and stable if fisheries move to new areas and exploit unfished stocks. Most assessments ignore much of the catch history in the Pacific before approximately 1960 primarily because detailed age- and (or) size-composition catch data are not available. Such assessments thus provide no basis for determining unfished stock sizes and depletion levels, which are critically important for developing fisheries policies. Because our model does not rely heavily on catch composition details, we were able to provide these estimates given the conservative assumption that early CPUE declines were indicative of changes in abundance.

Small tunas are difficult to identify to the species level and as a consequence some species may be underreported in catch data. This problem may be particularly severe for small bigeye tuna, which are consistently misclassified as small yellowfin or skipjack (Miyabe 1994). This may, in part, explain why the recruitment trends for small bigeye were similar to those of small yellowfin. Therefore, the recruitment trend for small bigeye may contain some artifacts of catch sampling errors.

Another known problem with the present analysis is that purse-seine fisheries setting on free-swimming tuna schools (i.e., unassociated sets) catch mainly large yellowfin. We could not distinguish among the various types of tuna setting practices or (worse) how they may have changed over time because only total purse-seine catch and effort data were available from the SPC database. Examination of more detailed SPC assessments for yellowfin in the western–central Pacific (Hampton and Fournier 2001*b*) indicated that unassociated set catches in the region bounded by 0°N to 20°N and 140°E to 150°W make up (approximately) 40% of the total purse-seine catches of yellowfin in that area. Unassociated set catches also increased at a similar rate as associated catches during the 1980s. Although the trends in fishing mortality may thus be adequately represented, separation of tuna purse-seine sets is probably an important detail that should be included in future aggregated analyses.

Blue marlin are also taken as bycatch in purse-seine fisheries. Based on preliminary estimates of bycatch (Lawson 1997) for the 1990s, however, these catches are more than an order of magnitude less than those taken in longlines (Cox et al. 2002). Further, purse-seine fishing activity did not really develop until the 1970s, long after the major CPUE decline of blue marlin had occurred. Therefore, purse-seine bycatch of blue marlin would have had little effect on our biomass trend estimates.

Although our results are generally consistent with those from other regions of the Pacific, the above uncertainties imply that biomass estimates should be treated with caution. Still, we were surprised by the fact that our estimates based on a relatively simple model and highly aggregated abundance index and catch data provided very similar estimates compared with much more detailed, data intensive assessments. This suggests that overall trends in abundance indices dominate the analysis and further details of age and (or) size composition of catches probably provide little additional information on impacts of fishing. Although we do not envision aggregated analyses replacing detailed ones, we do see several advantages to simpler approaches that should be exploited. For example, aggregated assessment models run orders of magnitude faster than highly complex ones. Speed of computation makes Monte Carlo testing and harvest policy simulations much more accessible. Thus, assessment and policy performance can be evaluated for various assumptions about how abundance indices are related to biomass. They can also be applied in a spatial context in which separate models may represent different populations. Such an ap-

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Table 4. Estimates of mean biomass for tunas and billfish in the central Pacific.

Species	Mean biomass ($kg \cdot km^{-2}$) 1952–1959	1990–1998	Biomass ratio
Large albacore	10.8	8.8	0.81
	5.2–22.3	4.3–17.8	
Small albacore	6.7	8.1	1.21
	4.3–10.4	5.2–12.6	
Large bigeye	16.4	6.9	0.42
	14.7–18.3	5.9–8.2	
Small bigeye	4.1	4.6	1.12
	3.5–4.8	3.8–6.2	
Large yellowfin	18.7	12.7	0.68
	14.4–24.2	8.9–18.2	
Small yellowfin	1.7	2.2	1.29
	1.3–2.4	1.8–2.9	
Skipjack	19.3	13.2	0.68
	5.5–67.7	4.9–47.2	
Blue marlin	2.8	0.6	0.21
	1.4–3.0	0.1–0.7	
Swordfish	1.3	0.6	0.56
	1.0–1.7	0.4–0.8	

Note: Approximate confidence limits (95%) are given below each estimate.

proach would be valuable for examining the impacts of fishery expansion across the Pacific as noted above.

Despite the relatively low biological productivity of the pelagic Pacific Ocean, tuna fisheries in this region have sustained increasingly large yields for the past five decades. In general, blue marlin, which is a larger, late-maturing species, tended to decline the most, whereas more productive (and valuable) species of tunas have been relatively resilient to increasing exploitation. Mean 1990s biomass of blue marlin may be as low as 20% of mean 1950s biomass, but for tunas, none appears to be below 40% of 1950s levels (Table 4). Although albacore declined for several years, current biomasses of both adults and juveniles appear close to or above historical levels. Similarly, juveniles of bigeye and yellowfin tuna may be experiencing a period of increased productivity in recent years and possibly going back to the mid-1970s.

Declines of top predators like blue marlin may be indicative of changes in other large pelagic predators such as sharks and other billfishes that are also taken as bycatch in longline fisheries (Lawson 1997). If such changes have occurred, then this could represent a substantial change in the trophic structure and predation regimes experienced by small tunas, which are important prey for these species. In Cox et al. (2002), we examine the extent to which observed recruitment and biomass trends of tunas described here can be explained by changes in trophic structure caused by fishing on these top predators.

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Reconstructing ecosystem dynamics in the central Pacific Ocean, 1952–1998. II. A preliminary assessment of the trophic impacts of fishing and effects on tuna dynamics

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Abstract: Pelagic fisheries in the Pacific Ocean target both large (*Thunnus* spp.) and small tunas (juveniles of *Thunnus* spp; *Katsuwonus pelamis*) but also take billfishes (*Xiphias gladius*, *Makaira* spp., *Tetrapturus* spp., *Istiophorus platypterus*) and sharks (*Prionace glauca*, *Alopias superciliosus*, *Isurus oxyrinchus*, *Carcharhinus longimanus*, *Galeocerdo cuvieri*) as bycatch. We developed a multispecies model using the Ecopath with Ecosim software that incorporated time-series estimates of biomass, fishing mortality, and bycatch rates (1952–1998) to evaluate the relative contributions of fishing and trophic impacts on tuna dynamics in the central Pacific (0°N to 40°N and 130°E to 150°W). The Ecosim model reproduced the observed trends in abundance indices and biomass estimates for most large tunas and billfishes. A decline in predation mortality owing to depletion of large predators was greatest for small yellowfin tuna and could possibly account for apparent increases in biomass. For other tunas, however, predicted changes in predation mortality rates were small (small bigeye) or were overwhelmed by much larger increases in fishing mortality (skipjack and small albacore). Limited evidence of trophic impacts associated with declining apex predator abundance likely results from the difficulties of applying detailed trophic models to open ocean systems in which ecological and fishery data uncertainties are large.

Résumé : Les pêches commerciales dans le Pacifique ciblent les thons, tant de grande (*Thunnus* spp.) que de petite taille (jeunes *Thunnus* spp.; *Katsuwonus pelamis*), mais elles récoltent aussi les espadons et les voiliers (*Xiphias gladius*, *Makaira* spp., *Tetrapturus* spp., *Istiophorus platypterus*), ainsi que les requins (*Prionace glauca*, *Alopias superciliosus*, *Isurus oxyrinchus*, *Carcharhinus longimanus*, *Galeocerdo cuvieri*) comme prises accessoires. Nous avons mis au point un modèle multispécifique basé sur le logiciel Ecopath additionné de Ecosim qui incorpore les séries temporelles d'estimations de la biomasse, de la mortalité due à la pêche et des taux de prises accessoires (1952–1998) pour évaluer les contributions relatives de la pêche et des impacts trophiques à la dynamique des populations de thons du centre du Pacifique (0°N à 40°N et 130°E à 150°O). Le modèle Ecosim reproduit les tendances observées des indices d'abondance et des estimations de biomasse chez les grands thons, ainsi que chez les espadons et les voiliers. Le déclin de la mortalité due à la prédation causée par l'épuisement des populations de grands prédateurs est maximal chez les petits albacores à nageoires jaunes et peut sans doute expliquer les augmentations apparentes de la biomasse. Chez les autres thons, cependant, les changements prédits de la mortalité due à la prédation sont ou bien faibles (petits thons ventrus), ou alors masqués par des augmentations beaucoup plus importantes de la mortalité due à la pêche (thonines à ventre rayé et petits germons). Les indications partielles qui laissent croire à l'existence d'impacts trophiques associés au déclin des prédateurs résultent sans doute des difficultés reliées à l'application des modèles trophiques détaillés à des systèmes océaniques ouverts, dans lesquels les données écologiques et halieutiques comportent de fortes incertitudes.

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Introduction

There is a growing tenor of attention paid to the ecological effects of fishing (NMFS 1999; Jackson et al. 2001) and an ecosystem approach to fisheries issues (NRC 1998) and its application in management. One approach to that objective is to meld the principles of single-species assessment models, which are hallmarks of fisheries science, with the more general modeling approaches that focus on trophic dynamics (Walters et al. 2000). Such a merger would allow attempts to determine the relative contributions of fishing and environmental factors as they affect trophic structure and fisheries production processes.

Pelagic tuna fisheries in the western and central Pacific (CNP; 0°N to 40°N and 130°E to 150°W; Fig. 1) are among the most productive and valuable fisheries in the world (FAO 1994). Despite highly intensive fisheries, most tuna stocks in the region have shown little negative impacts of fishing and some even appear to exhibit increasing recruitment over the past two decades (Hampton and Fournier 2001*a*, 2001*b*; Cox et al. 2002). However, the abundance of large piscivore species, which are generally less productive, have declined to varying degrees following nearly 50 years of targeted exploitation and bycatch in tuna-directed fisheries (Cox et al. 2002). Abundances of top predator fish species have declined in most marine ecosystems around the world mainly as a result of overexploitation (Pauly et al. 1998; Jackson et al. 2001). As a consequence of some of the most spectacular collapses, abundances of prey species and invertebrates have increased to unprecedented levels in response to reduced predation pressure from above (Lilly et al. 2000; Carscadden et al. 2001; Daskalov 2002). It is therefore possible that declines in CNP top predators could play an important role in observed increases of smaller tunas (*Thunnus* spp.) that constitute their prey.

In this paper, we develop an Ecopath with Ecosim (Walters et al. 2000) model of ecosystem dynamics in the CNP, which we use to evaluate the hypothesis that recent increases in albacore (*Thunnus alalunga*), bigeye (*Thunnus obesus*), and yellowfin (*Thunnus albacares*) tuna recruitment as suggested by single-species models (Cox et al. 2002) has been caused by changes in predation regimes. Previous work on multispecies, multigear fisheries in the CNP have focused on direct conflicts and interactions among various fishing fleets that target tunas (FAO 1994) and simulated keystone predator effects (Kitchell et al. 1999). This study employs an approach that sets the principles of single-species stock assessment in an ecosystem context as a basis for evaluating that which had been a very large unknown—predation as a component of natural mortality and the role of fishing mortality as a cause of changes in predation rates and abundance. Our approach identifies mortality owing to fisheries and that owing to predation and their dynamic interaction.

Methods

Ecopath model

Ecopath is a trophic mass-balance model that estimates a balance of trophic linkages based on specified biomasses, productivities, consumption rates, diet compositions, and fisheries yield for each food web component. Mathematically, this balance is represented by the following expression:

$$(1) \qquad B_i \cdot (P/B)_i \cdot EE_i = BA_i + Y_i + \sum_{j=1}^{n} B_j \cdot (Q/B)_j \cdot DC_{ji}$$

where B_i is the biomass (kg·km^{-2}) of group i, $(P/B)_i$ is the production-to-biomass ratio of group i, $(Q/B)_j$ is the consumption-to-biomass ratio of predators j that eat group i, and DC_{ji} is the average diet fraction of prey i for predator j. EE_i is the ecotrophic efficiency, or the fraction of total mortality that is accounted for by the modeled system, and Y_i are fisheries yields. The biomass accumulation term BA_i accounts for trends in absolute biomass during the period over which biomass estimates were made.

The CNP Ecopath model contains 25 living biomass pools and represents trophic conditions during the 1990–1998 period. Diet compositions for each group were updated from previously published CNP Ecopath models (Kitchell et al. 1999; Table 1). Published diet data were available for all tunas, billfishes, mahi mahi, lancetfish, and sharks. For the remaining groups, diet compositions were constructed based on habitat (epipelagic or mesopelagic) and relative predator–prey body sizes. Where only the general diet category "scombrids" was reported, we parsed the total among skipjack, small scombrids (*Euthynnus affinis*, *Auxis* spp.), small yellowfin, and small bigeye prey groups. A summary and bibliography for the diet matrix along with sources for *P/B* and *Q/B* values are available at http:\\www.limnology.edu\cnp_model.

Biomass and *P/B* values for large and small pools of albacore, bigeye, and yellowfin and total population biomass of skipjack (*Katsuwonus pelamis*), blue marlin (*Makaira* spp.), and swordfish (*Xiphias gladius*) were based on 1990–1998 averages estimated from single-species model assessments (Cox et al. 2002). Biomass and *P/B* values for blue sharks (*Prionace glauca*) were also based on single-species assessments (P. Kleiber, Southwest Fisheries Science Center, National Marine Fisheries Service, Honolulu, Hawaii, personal communication). All input biomass estimates represented averages over a year. Biomasses of all other groups were estimated by Ecopath given estimates of total yield, *P/B*, *Q/B*, and EE values (Table 2).

Total bycatches of nontarget biomass groups were determined from observer-based studies of longline and purse-seine fishery bycatch rates (Lawson 1997; Williams 1999). Bycatch of each group was calculated by multiplying group- and gear-specific bycatch proportions from the above studies by total yield for each gear type.

Where individuals in a population die at a constant instantaneous rate Z, *P/B* is equivalent to the instantaneous total mortality rate Z (Allen 1971). This equivalence applies regardless of the actual form of body growth (i.e., linear, exponential, asymptotic), which also contributes to total production (Allen 1971). We therefore set *P/B* values (Table 2) equal to total mortality rates $Z = F + M$, where F is the mean 1990s fishing mortality and M is the rate of natural mortality. The natural mortality rate M is then apportioned among predators after accounting for diet composition, predator and prey biomass, and consumption rates. Note that EE values

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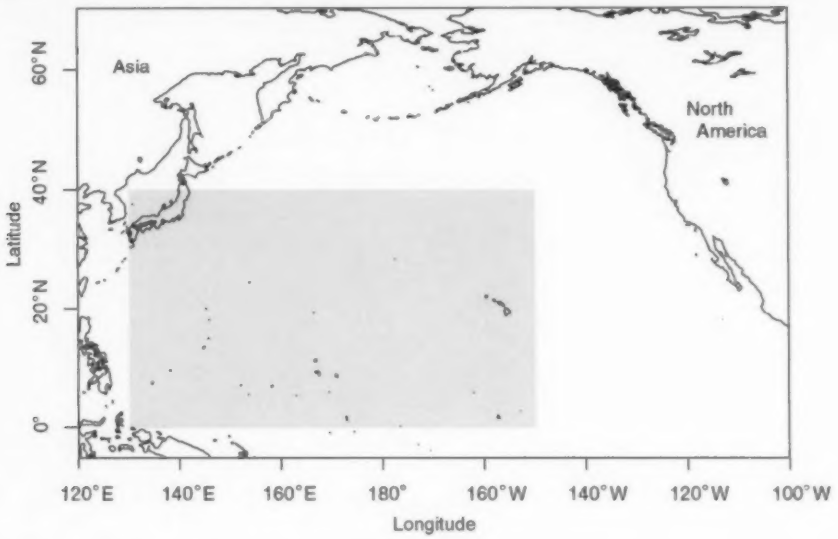
Fig. 1. Map of the Pacific Ocean with central north Pacific (CNP) represented by shaded area.



less than one indicate the actual proportion of M explained by the model.

Because estimates of fishing mortality in the CNP region were not available for groups taken as bycatch, we estimated P/B values from expected longevity, maximum age, or mean body size. Estimates of F were then calculated by dividing the total catch by the Ecopath biomass estimate. Natural mortality rate values for tunas were obtained from Hampton (2000) and Fournier et al. (1998). We assumed M values for blue marlin and swordfish were equal to 0.20 year^{-1}. Values of M for other groups were estimated from regression methods that incorporated maximum age (Hoenig 1983) or growth parameters (Pauly 1980).

Q/B (Table 2) for most groups was estimated from bioenergetics analyses (T. Essington, Marine Sciences Research Center, State University of New York–Stony Brook, Stony Brook, N.Y., unpublished data). Where data were not available for such analyses, we estimated Q/B from P/B using growth efficiencies between 10 and 20%. BA for albacore, bigeye, blue shark, and swordfish were estimated by regressing absolute biomass estimates from single-species assessments on year (1990–1998). All other BA values were assumed to be zero.

Ecosim model

We used the balanced CNP Ecopath model to parameterize a dynamic Ecosim model (Walters et al. 2000) that attempts to account for historical effects of fishing and changes in trophic structure. Fishing effort data (1952–1998) for each gear type were used to generate annual fishing mortalities for biomass pools that did not have fishing mortality estimates from our single-species analyses (Cox et al. 2002). This method involved first computing the fishing mortality rate imposed by fleet j on group i in the Ecopath base year as $F_{ji0} = Y_{ji0}/B_{i0}$, where Y_{ji0} is mean catch (1990–1998) of group i by fleet j, and B_{i0} is the mean biomass during the year (i.e., Ecopath biomass estimate). Then for each year in the Ecosim simulation, fishing mortality F_{jit} was computed as $F_{ji0}E_{jt}$, where E_{jt} is the fishing effort by fleet j in year t relative to the 1990–1998 mean effort. Annual fishing mortality estimates from the single-species analyses were used for all other groups because these accounted for some of the apparent changes in catchability over time (Cox et al. 2002).

Changes in natural mortality rates of prey groups are linked to changes in trophic structure through the Ecosim consumption equations and changes in biomasses of predators and prey (Walters et al. 2000). Consumption of prey i at time t is modeled as

$$(2) \qquad Q_{ij}(B_{it}, B_{jt}) = \frac{a_{ij}v_{ij}B_{it}B_{jt}}{(2v_{ij} + a_{ij}B_{jt})}$$

where a_{ij} is the rate of effective search for prey i by predator j and v_{ij} is the maximum predation mortality rate imposed on prey i in the presence of infinite predator biomass. The rate of effective search is calculated from the Ecopath estimates of Q_{ij0}, B_{i0}, and B_{j0}. The Ecopath base predation mortality rate of prey group i caused by predator j is $M_{ij0} = Q_{ij0}/B_{i0}$. Values for "vulnerability" parameters v_{ij} are set by applying multipliers k_{ij} [1, ∞] such that

$$(3) \qquad v_{ij} = k_{ij}M_{ij0}, \quad k_{ij} > 1$$

In other words, vulnerability parameters specify the upper limit of predation mortality rates for each predator–prey interaction. Setting v_{ij} involves the following transformation from k^*_{ij} [0, 1] (set by the user) to k_{ij} [1, ∞] in eq. 3:

$$k_{ij} = \frac{1 - k^*_{ij}}{1 + k^*_{ij}}$$

For example, setting $k^*_{i\cdot}$ ("·" indicates vulnerability to all predators) to 0.35 in the Ecosim interface implies that predation mortality on prey i can increase to a maximum of 2 times the base predation mortality rate estimated from Ecopath, regardless of how abundant predators might be-

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Table 1. Diet composition matrix for central north Pacific (CNP) Ecopath model.

	Predator																					
Prey	LB	SB	LY	SY	LA	SA	LBS	SBS	BM	LS	BS	SW	OB	MM	SS	FS	SK	LAN	SQ	FF	MF	EF
LB	—	—	—	—	—	—	—	—	—	*	—	—	—	—	—	—	—	—	—	—	—	—
SB	*	—	*	—	*	—	—	—	0.04	0.05	0.02	0.03	0.01	—	—	—	—	—	—	—	—	—
LY	—	—	—	—	—	—	—	—	—	0.01	0.01	—	*	—	—	—	—	—	—	—	—	—
SY	*	—	*	—	*	—	—	—	0.10	0.15	0.02	—	0.10	—	—	—	—	—	—	—	—	—
LA	—	—	—	—	—	—	—	—	—	0.01	—	*	—	—	—	—	—	—	—	—	—	—
SA	*	—	*	—	*	—	—	—	*	0.02	0.01	*	0.01	—	—	—	—	—	—	—	—	—
LBS	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
SBS	—	—	—	—	—	—	*	—	—	0.09	—	—	—	—	—	—	—	—	—	—	—	—
BM	—	—	—	—	—	—	—	—	—	0.01	—	—	—	—	—	—	—	—	—	—	—	—
LS	—	—	—	—	—	—	—	—	—	0.01	—	—	—	—	—	—	—	—	—	—	—	—
BS	—	—	—	—	—	—	—	—	—	0.02	0.01	—	—	—	—	—	—	—	—	—	—	—
SW	—	—	—	—	—	—	—	—	0.01	0.01	—	—	—	—	—	—	—	—	—	—	—	—
OB	—	—	—	—	—	—	—	—	0.01	0.02	—	—	—	—	—	—	—	—	—	—	—	—
MM	*	—	0.01	—	*	—	—	—	0.10	0.05	0.02	0.01	0.05	0.01	—	—	—	—	—	—	—	—
SS	0.06	0.01	0.35	0.16	0.10	0.05	—	—	0.28	0.24	0.17	0.06	0.10	0.19	—	—	0.25	—	—	—	—	—
FS	0.13	0.05	—	—	0.15	0.15	0.35	0.10	—	0.02	0.05	0.43	—	0.05	—	—	—	—	—	—	—	—
SK	*	0.03	0.05	0.03	0.03	—	—	—	0.23	0.11	0.02	—	0.15	—	—	—	*	—	—	—	—	—
LAN	0.05	0.05	—	—	0.05	0.03	—	—	—	0.02	0.03	0.03	—	—	—	—	—	0.05	—	—	—	—
SQ	0.15	0.20	0.10	0.15	0.20	0.25	0.20	0.45	0.05	0.05	0.30	0.18	0.30	0.05	0.20	0.20	0.15	0.20	—	—	—	—
FF	—	—	0.10	0.15	—	—	—	—	—	—	—	—	—	0.40	—	—	—	—	—	—	—	—
MF	0.33	0.29	0.11	0.15	0.20	0.10	0.25	0.25	—	0.04	0.16	0.19	—	0.01	0.10	0.04	0.05	0.50	0.06	—	—	—
EF	0.10	0.07	0.17	0.15	0.14	0.25	0.10	0.10	0.17	0.08	0.16	0.08	0.28	0.15	0.20	0.06	0.25	0.05	0.04	—	—	0.01
EMN	0.05	0.15	0.05	0.10	0.05	0.07	0.05	0.05	—	0.01	0.02	—	—	0.10	0.35	0.30	0.20	—	0.40	1.00	1.00	0.99
MMN	0.10	0.15	0.05	0.10	0.07	0.10	0.05	0.05	—	0.01	0.01	—	—	0.05	0.15	0.40	0.10	0.20	0.50	—	—	—
PP	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

Note: Asterisk (*) indicates diet composition (DC) greater than zero but less than 0.01. See Table 2 for group codes. Epipelagic micronekton (EMN) and mesopelagic micronekton (MMN) diets both consist entirely of phytoplankton (DC = 1.00).

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Table 2. Balanced Ecopath estimates of trophic level (TL), biomass (B; kg·km^{-2}), production per biomass (P/B; year^{-1}), consumption per biomass (Q/B; year^{-1}), ecotrophic efficiency (EE), total yield from all fisheries (Y; kg·km^{-2}), and mean 1990s fishing mortality (F; year^{-1}).

Group	Code	TL	B	P/B	Q/B	EE	Y	F
Large bigeye	LB	4.06	8.80	0.42	7.20	**0.332**	1.28	0.15
Small bigeye	SB	3.82	4.20	0.67	9.70	**0.233**	0.35	0.08
Large yellowfin	LY	4.12	12.66	0.98	14.00	**0.179**	2.16	0.17
Small yellowfin	SY	3.91	2.25	2.52	17.60	**0.736**	2.77	1.23
Large albacore	LA	4.10	8.80	0.36	7.30	**0.437**	0.49	0.06
Small albacore	SA	3.96	8.12	0.35	9.60	**0.580**	1.27	0.16
Large blue shark	LBS	4.05	4.96	0.32	2.75	**0.989**	0.99	0.20
Small blue shark	SBS	3.99	0.35	0.46	3.50	**0.504**	0.02	0.06
Blue marlin	BM	4.61	0.58	0.46	4.00	**0.700**	0.18	0.31
Large sharks	LS	4.68	**0.28**	0.39	2.50	0.500	0.05	0.19
Brown sharks	BS	4.32	**1.67**	0.18	2.80	0.600	1.02	0.08
Swordfish	SW	4.32	0.87	0.60	5.00	**0.653**	0.33	0.37
Other billfish	OB	4.41	**0.81**	0.44	5.00	0.600	0.18	0.23
Mahi mahi	MM	3.97	**11.23**	0.85	20.00	0.600	0.42	0.05
Small scombrids	SS	3.53	**263.90**	1.08	10.00	0.700	—	—
Flying squid	FS	3.32	**19.93**	7.13	50.00	0.350	0.70	0.04
Skipjack	SK	3.85	13.20	2.90	20.00	**0.771**	14.12	1.07
Lance	LAN	3.89	**49.44**	0.47	2.90	0.770	—	—
Squids	SQ	3.10	**1 482.82**	3.07	25.00	0.200	—	—
Flying fishes	FF	3.00	**53.35**	2.38	10.00	0.900	—	—
Mesopelagic fish	MF	3.05	**9 156.06**	2.12	6.00	0.200	—	—
Epipelagic fish	EF	3.00	**4 611.67**	1.66	6.00	0.300	—	—
Epipelagic micronekton	EMN	2.00	**36 844.48**	5.52	50.00	0.400	—	—
Mesopelagic micronekton	MMN	2.00	**6 325.83**	5.62	35.00	0.550	—	—
Phytoplankton	PP	1.00	**26 583.78**	194.36	—	0.400	—	—

Note: Code entries indicate the letter codes used for diet matrix in Table 1. Values in bold type were estimated using Ecopath mass-balance solution.

come. Alternatively, setting $k_{i,}^{*}$ equal to 0.001 causes predation mortality to remain nearly constant at the Ecopath level. For the CNP simulations, reasonable settings for $k_{i,}^{*}$ values were determined by first setting $k_{\cdot,}^{*}$ ("·" indicates all predator–prey interactions) values to 0.50, which means that predation mortality rates could increase to a maximum of approximately 3.6 times the Ecopath values. Values were then adjusted for each species as needed until a sum of squares criterion between catch-per-unit-effort (CPUE; see below) and biomass was minimized. Such solutions may only be local minima, however, because no formal nonlinear parameter search was done. In general, model fits were most sensitive to the extremes in which predation mortality was either constant $k_{i,}^{*} = 0.001$ or moderately variable $k_{i,}^{*} = 0.50$.

Two additional problems needed to be overcome before simulating CNP ecosystem dynamics from 1952 to the present. First, we did not have reliable diet information or bycatch estimates from the 1950s. Both Ecopath and Ecosim simulations are highly sensitive to the initial diet matrix because these determine the base predation mortality rates in eq. 3 and rates of effective search for prey by predators in eq. 2. Bycatch inputs determine the initial fishing mortality rates, which are then adjusted annually in Ecosim according to the method described above. The simplest assumption, and one which is commonly recommended, is to use the 1990s diets as a first guess for 1950s diets. However, if biomass of a given prey i has changed between the two time periods, then this assumption is only valid if the search rate for prey i by predator j is inversely proportional to the abundance of prey i. For example, a twofold increase in prey biomass must be accompanied by an exact twofold decrease in predator search rate for that prey if the predator's diet composition is to remain constant. This contradicts eq. 2, which assumes that search rates are constant. Because Ecosim assumes constant search rates, predator diet compositions change in response to changes in prey abundance. Therefore, for fixed model parameters and forcing inputs (i.e., fishing mortality rates), the consumption equations in Ecosim eq. 2 imply deterministic changes in diet compositions for all time periods. Therefore, we must use 1950s diet compositions that are consistent with Ecosim predictions based on predator and prey biomass implied for that time.

Our approach to dealing with this issue was to use the 1990s Ecopath model as an initial state from which we reconstructed the (implied) 1950s trophic state. Calculating the implied 1950s trophic state is analogous to the concept of unfished stock size in single-species assessment. That is, the fixed set of Ecopath parameters and fishing mortality rates act like stock–recruitment and natural mortality parameters in single-species theory and determine the equilibrium trophic state in the absence of fishing. To generate the unfished or lightly fished 1950s state, we set the first simulation year in Ecosim to 1928 and all relative fishing effort and fishing mortality rates to 1952 values. Running the CNP Ecosim model from 1928 to 1951 under this fishing regime allowed the model ecosystem to move from a 1990s state to

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a new equilibrium that was assumed to represent the biomasses, production rates, and diet compositions during the early 1950s. From 1952 to 1998, we then set the relative fishing efforts by fleet and year as described above to fishing mortality estimates from the single-species analyses. The main benefit of this approach is that (unknown) diet compositions and biomasses for the 1950s remain consistent with those implied by the 1990s Ecopath model. Therefore, it was more likely that the long-term simulation would at least reproduce the 1990s Ecopath state for a wide range of Ecosim parameters. Using arbitrary diet values, 1990s values, or "educated" guesses would most likely lead us to setting predation interaction parameters (k^*) that reproduce the 1990s state, but we would not be able to determine whether they imply strong or weak interactions, or just counteract bad assumptions. Our criteria for determining how well the above initialization scheme worked was to judge whether Ecosim biomasses approached 1950s (i.e., single-species estimates) levels under the 1952 fishing mortality rates, and then 1990s levels following application of historical fishing rates. In most cases, biomass predictions passed through 1950s and 1990s levels for a range of k^* values, and this allowed us to focus further parameter testing on the transient dynamics in between (i.e., 1952 to 1998).

The second issue involved controlling strong cyclic dynamics of small yellowfin as predicted from the initial model. Ecosim offers a "feeding time adjustment" parameter that determines how a given group adjusts time spent feeding (and thus exposure to predation risk) in response to changes in prey availability. Setting the "feeding time adjustment" parameter in Ecosim for small yellowfin to 0.2 eliminated this behaviour. Setting this parameter equal to zero, 0.2, or 0.5 did not change the overall biomass trends shown below; it simply removed the distracting cyclic dynamics.

Ecosim predictions for groups included in the single-species assessments were compared with CPUE data that best reflected patterns of change in biomass (Cox et al. 2002). Most of these groups were also split into small and large components, as was done in single-species analyses (Table 3). Longline CPUE data were used for all adult tunas, billfishes, and blue sharks; other-gear CPUE for skipjack, small yellowfin, and small bigeye; and troll CPUE for small albacore. All CPUE data were scaled to the mean biomass predictions given by Ecosim simulations. Corresponding fits between gear-specific CPUE and biomasses of tunas and billfish are given in Cox et al. (2002).

Results

Total catch estimates extrapolated from bycatch proportions were of similar magnitude to catches of groups for which we had more reliable data. For example, total longline catch of other billfishes (*Tetrapturus* spp., *Istiophorus platypterus*) was nearly identical to that of blue marlin, and brown shark (*Carcharhinus plumbeus*) catch in longline fisheries was similar to that of large blue sharks (Table 2). Fishing mortality rate estimates for groups taken as bycatch ranged from 0.05 year^{-1} (mahi mahi) to 0.23 year^{-1} for other billfish.

The Ecosim model predicted general patterns of biomass change for apex predators relatively well compared with observed data and estimates from single-species analyses (Figs. 2*a*, 2*b*, and 2*d*). However, for blue marlin and swordfish, Ecosim predicted somewhat lower depletion compared with single-species models (Table 4). Simulated declines for groups consisting of other billfishes (Fig. 2*c*) and all sharks combined (Fig. 2*e*) were similar to those for which time-series CPUE data were available.

Table 3. Ecosim parameter settings for tuna groups that were split between juvenile and adult pools.

Group	a_k (year)	$w_{adult}:w_{recr}$	K (year^{-1})
Albacore	5	1.54	0.41
Bigeye	4	1.50	0.39
Yellowfin	2	2.78	0.47

Note: a_k, age-at-recruitment to adult; $w_{adult}:w_{recr}$, ratio of mean adult body mass to body mass at recruitment to adult; K for the von Bertalanffy growth function expressed in terms of body mass.

Changes in biomass of apex predators had almost no direct effect on predation rates and dynamics of adult tunas because Ecopath predation mortality rates were minimal or nearly zero (i.e., EE values in Table 2 are very close to fishing mortality divided by P/B). Therefore, most of the dynamics predicted for adult tunas derive from direct fishing impacts and deterministic changes in simulated recruitment.

Similar to the single-species analysis, dynamics of large albacore in Ecosim (Fig. 3*a*) were largely dominated by the impacts of fishing on small albacore (Fig. 4*a*) because simulated changes in predation mortality on small albacore needed to be low ($k_i^* < 0.20$) to match the observed CPUE data and single-species estimates. Because juvenile and adult albacore fluctuated in opposing cycles from 1928 to 1952, biomass of juveniles was lower in the 1950s relative to the single-species estimates. This resulted in the depletion ratio of 1.98 predicted by Ecosim compared with 1.21 from single-species (Table 4).

The Ecosim model predicted the overall decline of large bigeye tuna (Fig. 3*b*; $k_{.j}^* = 0.50$ as predator); however, no trophic- or fishing-impact hypothesis could explain the changes in small bigeye biomass as indicated by single-species results (Fig. 4*b*; $k_{i.}^* = 0.20$ as prey). Final k^* settings were chosen so that the 1950s and 1990s mean biomasses approximately matched the single-species results for adults (Table 4). Setting $k_{i.}^*$ values for small bigeye to reflect strong predator control ($\geq$0.50) resulted in 1950s biomass levels that were much lower than those estimated from single-species analyses. Even under this strong predator–prey interaction hypothesis, small bigeye biomass did not exhibit changes that were consistent with the data. The lack of response to trophic changes in part reflects low EE values, that is, small bigeye were not strongly represented in the diets of any particular predator so that only a small proportion of small bigeye mortality is explained by Ecopath predator groups. Also, Ecosim did not predict increases in predation mortality during the 1950s when estimated recruitment of small bigeye was declining. Therefore, overall changes in predation mortality were minimal (Fig. 5*a*).

For large yellowfin, Ecosim predicted slightly lower 1950s biomass but generally higher biomass over most of the modeled time period (Fig. 3*c*). Also, Ecosim suggested that large yellowfin biomass increased since the 1950s in contrast to the single-species results, which indicated an overall decline

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Fig. 2. Predicted changes in biomass of apex predator groups: (*a*) blue marlin (*Makaira nigricans*); (*b*) swordfish (*Xiphias gladius*); (*c*) other billfish (*Makaira* spp., *Tetrapturus* spp., *Istiophorus platypterus*); (*d*) blue sharks (*Prionace glauca*); (*e*) large and brown sharks combined (*Alopias superciliosus*, *Isurus oxyrinchus*, *Carcharhinus longimanus*, *Galeocerdo cuvieri*). Observed catch-per-unit-effort (circles; broken line) and predicted biomass for single-species assessment (thin line) and Ecosim (thick line) models.

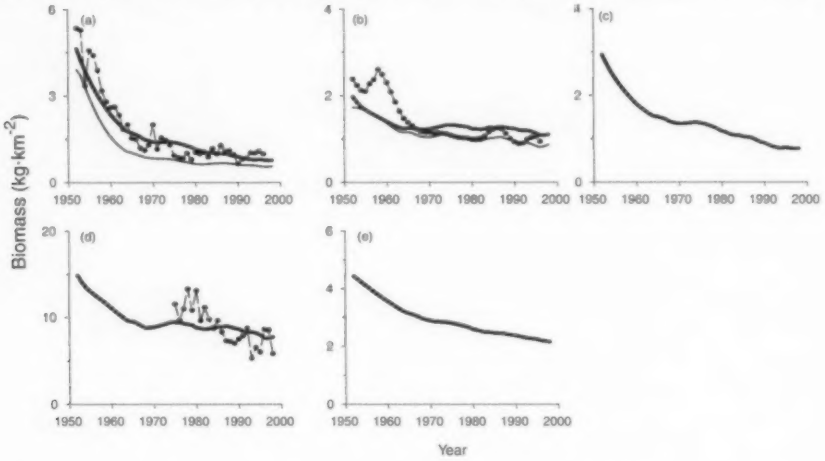

Table 4. Comparison of estimated changes in biomass of central north Pacific tunas and billfish between single-species and ecosystem models.

	Biomass ratio	
Biomass group	Single-species	Ecosim
Large albacore	0.81	0.79
Small albacore	1.21	1.98
Large bigeye	0.42	0.39
Small bigeye	1.12	0.67
Large yellowfin	0.68	1.06
Small yellowfin	1.29	0.95
Skipjack	0.68	0.59
Blue marlin	0.21	0.23
Swordfish	0.56	0.68

Note: Biomass ratios are mean biomass during 1991–1998 period divided by mean biomass over 1952–1959 period.

(Table 4). Both Ecosim and the single-species estimates agreed that small yellowfin biomass increased since the 1960s, and the magnitude of changes was similar (Fig. 4*c*). However, Ecosim also suggested that small yellowfin declined continuously between the 1950s and early 1970s so that overall, biomass during the 1990s was lower than in the 1950s (Table 4). In Ecosim, the increase in small yellowfin biomass occurred as a result of decreased predation mortality rates ($k_i^* = 0.50$) imposed mainly by sharks and to a lesser degree by billfishes (Fig. 5*b*). A steady increase in fishing mortality over the entire modeled period was more than offset by these declines in predation mortality.

Simulated biomass of skipjack also compared well with observed CPUE and single-species estimates. Applying high ($k_i^* = 0.50$; value used for Fig. 4*d*) or low ($k_i^* = 0.001$) vulnerability values did not change the general trend in biomass or the predicted response to fishing. The low value produced higher simulated biomasses during the 1952–1982 period; however, these were well within the range of uncertainty associated with skipjack biomass from the single-species model (Cox et al. 2002). Most of the change in predation mortality of skipjack was due to all tunas, which included cannibalism (Fig. 5*c*). However, the overall change in predation mortality was small and changes in total mortality were dominated by large increases in fishing mortality.

The brief but sharp decline of skipjack caused a substantial increase in the biomass of small scombrids, which increased to approximately 1.5 times 1950s levels (Fig. 4*e*). As a result of this increase, the predicted proportion of small scombrids in large yellowfin tuna diets increased from 26% in the 1950s to a peak of more than 40% during the 1990s. This change demonstrates the point that we made earlier (i.e., reasons for using 1990s model and diets as a base in Methods section) that diet fractions between two widely separated periods might differ substantially as a result of changes in predator and prey biomasses. The empirical diet composition used for the 1990s was 35% (Table 1), which is approximately the simulated average diet over the 1990s. The only other notable response to changes in predator biomass occurred for flying squid, which increased following the decline of large bigeye tuna (Fig. 4*e*).

Discussion

Our objectives in this paper were to test Ecosim model predictions against observed abundance indices and single-species estimates and to examine how fisheries could affect the food web structure and recruitment of tunas in the central north Pacific. Ecosim performed reasonably well for most groups in the model for which we had time-series data for comparison and estimated fishing mortality rates. In several of these cases, correspondence between the model and other data was not strongly affected by alternative specifications of trophic interaction parameters (i.e., k^* values). This suggests that the basic structure provided by Ecopath, partic-

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Fig. 3. Predicted changes in biomass of adult tunas: (*a*) large albacore (*Thunnus alalunga*); (*b*) large bigeye (*Thunnus obesus*); (*c*) large yellowfin (*Thunnus albacares*). Observed catch-per-unit-effort (circles; broken line) and predicted biomass for single-species assessment (thin line) and Ecosim (thick line) models.

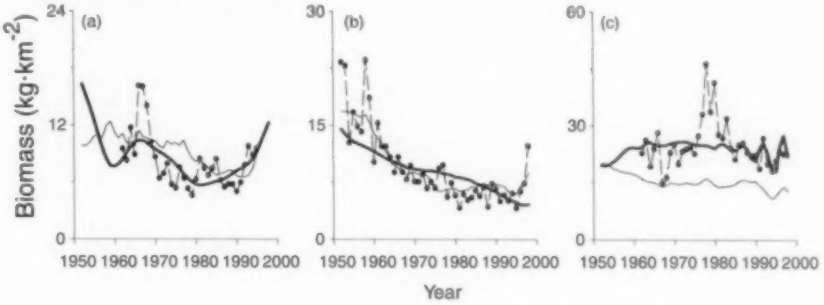
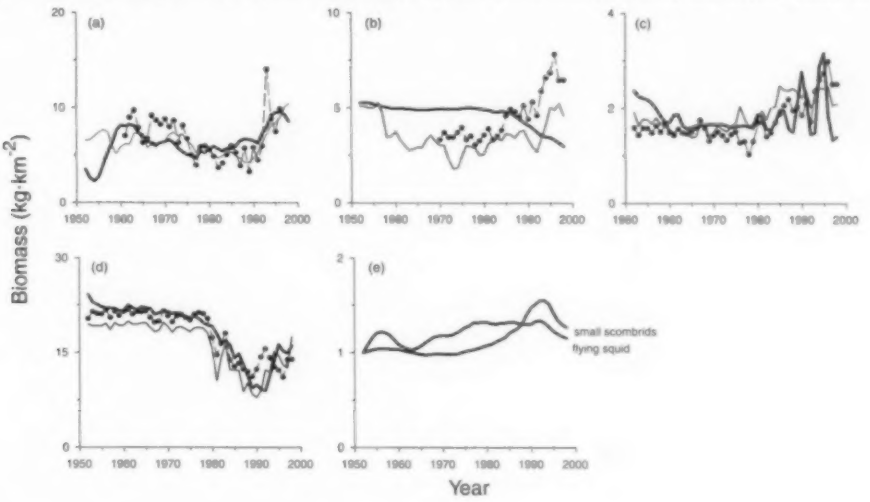


Fig. 4. Predicted changes in biomass of small tunas and major prey groups: (*a*) small albacore (*Thunnus alalunga*); (*b*) small bigeye (*Thunnus obesus*); (*c*) small yellowfin (*Thunnus albacares*); (*d*) skipjack (*Katsuwonus pelamis*); (*e*) small scombrids (*Euthynnus affinis*; *Auxis* spp.) and flying squid (*Ommastrephes bartrami*) (biomasses relative to 1952–1959 mean). Also shown are observed catch-per-unit-effort (circles; broken line) and predicted biomass from single-species assessment (thin line) and Ecosim (thick line) models.



ularly the diet composition matrix and *P/B* values, tend to have a strong influence on the model dynamics and responses to fishing predicted by Ecosim.

Depletion of apex predators, owing mainly to bycatch in tuna-directed fisheries, was hypothesized to have caused decreases in predation mortality and consequent increases in biomass of juvenile albacore, bigeye, and yellowfin tunas or greater resilience to fishing for skipjack. However, major impacts of changes in predation mortality rates for most tuna groups were either poorly determined or so small as to seem insignificant given the complexity of the model and quality of the data.

For small albacore, predicted changes in predation mortality were minimal, suggesting that the observed dynamics were dominated mainly by direct fishing impacts upon juveniles. This conclusion most likely reflects the degree of spatial separation between small albacore and most of the major predators in the model. Small albacore mainly occupy transition-zone waters along the northern edge of the CNP area. Therefore, this group does not appear as a major component in the diets of apex predators.

Bigeye tuna were the most problematic, and we could not determine whether predation mortality changes have been important. This was the main case in which the model was sensitive to alternative predation interaction parameters; however, none of those tested provided a reasonable model fit. There are several possible causes for such a failure. As we acknowledged in the single-species analysis (Cox et al. 2002), the catch and effort data for both small and large bigeye tuna contain problems with misclassification (small bigeye) and important changes in effective fishing effort (large bigeye). Also, as noted below, bigeye may be strongly affected by fishing or environmental effects outside the CNP area because the Pacific-wide stock is generally considered to be a single unit. Although we could not tell how important these problems were from the single-species perspective (although we knew they existed), the failure of the model to represent either fishing or potential trophic effects leads us to believe

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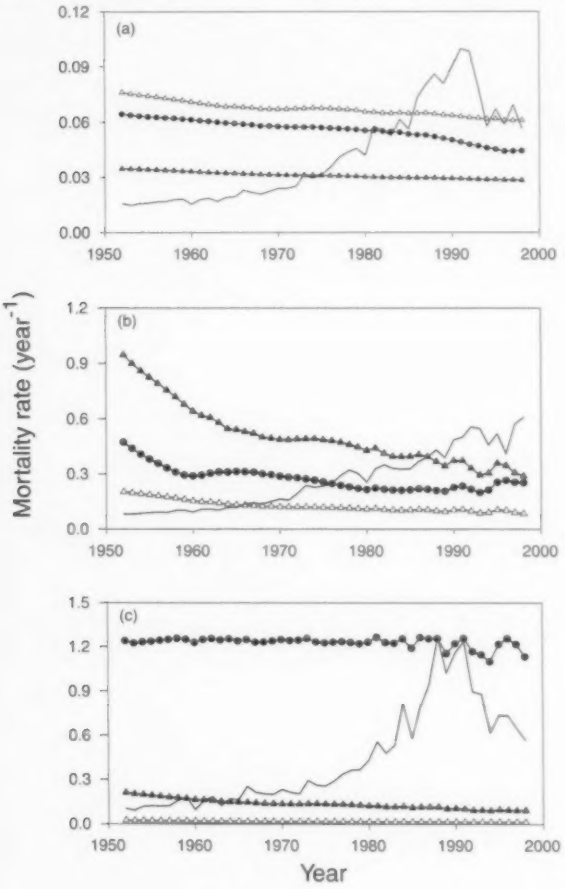
Fig. 5. Predicted changes in fishing (solid lines) and predation mortality of (*a*) small bigeye (*Thunnus obesus*), (*b*) small yellowfin (*Thunnus albacares*), and (*c*) skipjack (*Katsuwonus pelamis*). Predation mortality components were summed over all billfish (open triangles), all sharks (solid triangles), and all tunas (circles).



that our original single-species results are suspect or that bigeye are particularly sensitive to environmental forces. A possible biological cause for the Ecosim model failure is the fact that we used an age-at-recruitment of 4 years for bigeye, which is twice that used for yellowfin. Although this is generally accurate as the age at which bigeye begin to contribute substantially to total reproduction (our main reason for using this age), it may be too crude a representation of the scale at which predation impacts are important. An age of 4 years leads to greater sensitivity to predation impacts because fish are subject to predation for longer times (i.e., 4 years instead of 2). However, by age 4 bigeye likely outgrow vulnerability to many predators, and this is reflected in the weak representation in predator diets and low Ecopath EE values. Future versions of Ecopath and Ecosim will incorporate a wider range of juvenile age–size stanzas and this may help in cases where strong size-dependent predation interactions exist.

Yellowfin tuna were the only case in which predicted changes in predation mortality were large enough to cause noticeable increases in biomass. Ecosim predictions for small yellowfin fit the observed CPUE data and single-species results reasonably well for a range of predation parameter values, particularly from the early 1970s to the present. In contrast to the single-species estimates for large yellowfin that indicated a decline, Ecosim predicted an overall increase in biomass of large yellowfin since the 1950s. However, the fit to longline CPUE data did not appear to be any better or worse than that predicted by the single-species analysis.

Ecosim performed well over a range of parameter values for skipjack, mainly because fishing mortality increases were very large compared with predicted changes in predation mortality. For example, total predation mortality decreased by approximately 0.2 M, whereas fishing mortality increased by 0.8 M. Therefore, it seems that any changes in predation mortality on skipjack would be difficult to detect.

Although our preliminary results are encouraging in some respects, there are several major uncertainties associated with the present analysis. The first, of course, is that the ecosystem analysis, like the individual single-species assessments upon which it is based, relies on relatively poor quality, fishery-dependent data that are known to contain a myriad of biases and problems. Also, the diet information and bycatch rates are based upon small samples from limited spatial and temporal scales. We make no pretense that going into more trophic detail has in any way reduced the uncertainty associated with poor quality data. On the contrary, our ecosystem dynamics assessment is almost guaranteed to be more uncertain than estimates from single-species analyses because many more uncertain parameters have been introduced without substantially increasing the amount of information from which to determine plausible parameter values. For example, the Ecopath diet matrix, which has substantial effects upon dynamic model predictions, is rarely known with a high degree of certainty. Still, the ecosystem approach has been valuable in that most observations are either consistent with trophic- (yellowfin) or fishing-impact (albacore, skipjack) hypotheses or else are inconsistent with any hypothesis (bigeye).

Second, tunas and billfishes, which have the strongest empirical basis in the model, typically occupy large tracts of ocean that cannot easily be divided into smaller, more manageable scales. As a result, the scale needed to model their dynamics includes many different types of ecosystems. For example, skipjack and yellowfin tunas typically occupy tropical zones with characteristic fauna, whereas species such as albacore occupy cooler waters along the northern subtropical–subarctic transition zone. In some respects, such issues do not represent major difficulties because the diet composition estimates implicitly represent such differences in spatial areas occupied. For example, major changes in biomass of albacore tuna caused little noticeable impact on more tropical species because the tropical ones are not represented in albacore diets.

An area as large as CNP also exhibits a range of spatially distinct environmental influences that we did not include in the model. Although Ecosim has the capability to examine environmental forcing hypotheses, we could find no justifi-

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cation for incorporating these into the model based on the limited scope and quality of the data.

Third, an important factor that was left out of the model is the fact that many of these species migrate long distances, and it is quite likely that several migrate into and out of the model area. Ecopath generally assumes that the system is closed, and it is highly likely that we have violated such an assumption. Although migration distance of individual tunas is potentially large, the general consensus among tuna migration researchers is that most fish remain within a few hundred miles of their origin (Suzuki 1994; Wild 1994). Even moderate movement or influx from areas just south of the equator could affect tuna catches and abundances indices in the CNP. Most of catches, particularly for skipjack and yellowfin, derive from areas along this southern boundary of the CNP area. However, tagged skipjack and yellowfin in this area appeared to remain north of the equator and east of 130°E (Hampton et al. 2000; Hampton and Fournier 2001*a*), so that the overall impact of movement may not be substantial at the larger CNP scale. Bigeye, on the other hand, tend to migrate much larger distances and are generally considered a single Pacific-wide stock for formal stock assessment purposes (Hampton and Fournier 2001*b*). Therefore, it is quite likely that bigeye will continue to be problematic in a context such as this where we only consider a limited area of the Pacific.

Fourth, we chose to leave marine mammals out of the model. Our choice for doing so was that we had little information with which to parameterize the trophic impacts of these groups. However, to say that we have ignored their impacts completely is incorrect: EE values less than one for all groups indicate that some mortality (possibly owing to marine mammals) remains unexplained by the model. The degree of error resulting from such an omission primarily depends upon the degree of variation in groups responsible for unmodeled mortality components. We have little basis upon which to judge how marine mammal populations have changed over the past five decades in the CNP. However, fisheries such as the high-seas driftnet and purse-seine sets on tuna schools associated with marine mammals have likely impacted marine mammal populations and could have thus caused changes in predation mortality rates of several groups. Inclusion of marine mammals should therefore be considered an important priority for future versions of the CNP model.

Finally, many of these species are opportunistic feeders with relatively high consumption rates. Opportunistic feeding behaviour is probably crucial to the success of tunas in low productivity oceans, but it probably reduces our ability to detect significant trophic impacts from poorly measured indices. Even small diet fractions can be critically important to the dynamics of a prey species if the predator biomass is large (i.e., yellowfin). This could have major implications for species that seldom appear in predator diets, or worse, those that are not considered "interesting" to biologists.

Although our long-term simulations remain uncertain (and the above is certainly not an exhaustive listing), comparison with historical data is crucial if ecosystem model predictions are to be evaluated objectively. There is simply no basis upon which to determine the credibility of any model that has not been shown to reproduce historical dynamics. A model that does so despite several layers of quantitative or qualitative uncertainty at least provides a starting point for determining what types of data are needed to move forward or where key uncertainties exist. Even model solutions that do reproduce past changes are still not likely to be unique and ours is no exception: ecosystem models in general tend to be overparameterized in the sense that many parameter combinations explain the observed data equally well.

Depletion of apex predators from most ecosystems around the world represents an experiment from which we expect to see increasing biomass and yields at lower trophic levels. Fishing down major groundfish species has been implicated in increases of shrimp (Lilly et al. 2000) and capelin (Carscadden et al. 2001) in the northwest Atlantic and reduced spatial overlap between Georges Bank groundfishes and their prey (Garrison and Link 2000). At the extreme, large-scale removal of top predators can invoke a cascade of trophic changes extending all the way to primary production (Daskalov 2002). Despite all of the evidence for trophic impacts of fishing in closed seas and coastal areas, however, we had difficulty detecting any substantial ecosystem-scale impacts of fishing in the pelagic Pacific. Although the ecosystem model appeared to represent apex predator declines relatively well compared with the single-species assessments, such declines may not have been strong enough to cause the large changes seen in other more disturbed systems. On the other hand, our CNP model is based upon data that is aggregated over large spatial scales, fish species, and age structures so it is not entirely surprising that the model fails to exhibit highly responsive behaviour. The combination of such factors may represent a serious barrier to the application of whole-ecosystem approaches to pelagic oceans.

The inclusion of time-series data, updating consumption rate estimates based on bioenergetics, and a more extensive survey of the diet literature represents a vast improvement over previous CNP ecosystem models based on far more uncertain Ecopath models alone (Kitchell et al. 1999). However, this improvement did not change the general conclusion of Kitchell et al. (1999) that no particular species or group in the CNP stands out as a keystone predator. Such a conclusion remains uncertain because the CNP Ecopath and Ecosim models are strongly based on biomass estimates of high trophic levels where the impacts of slow, long-term changes in predation regimes might be least detectable. A notable change in biomass at lower trophic levels occurred for small scombrids as predation mortality by skipjack decreased during their relatively brief decline. Although catch and effort data exist for small scombrids, such data are not considered very reliable because of a lack of reliable annual catch statistics and targeted fisheries; however, these conditions may be improving (FAO 1994).

The most revealing result in this study was the response of yellowfin tuna to increasing fishing mortality rates. Most stock assessments agree that yellowfin tuna experienced a period of increasing recruitment during the 1980s when fishing mortality was at an all-time high (IATTC 1991; Hampton and Fournier 2001*a*; Cox et al. 2002). However, stock assessments suggesting that recruitment increases with increasing fishing mortality are usually viewed with skepticism and this was the

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main reason for investigating the potential causes. We have shown that increasing yellowfin tuna recruitment is consistent with estimated declines of apex predators. Although single-species analyses may correctly estimate such an increasing trend, they cannot predict recruitment rates in the future, or how recruitment might change in response to changes in fishing practices. For example, our analysis suggests that billfishes and sharks are currently at low abundance and impose low predation pressure on small yellowfin. In the future, however, fishing mortality rates on these groups may decrease because of increasing pressure to reduce longline bycatch. If such attempts prove successful, then our model would predict rather substantial declines in yellowfin tuna biomass independent of targeted fishing mortality rates. These types of indirect interactions among fisheries are a serious concern among pelagic fisheries management agencies, and the ecosystem modeling approach at least provides a way to assess potential indirect impacts of alternative fishing regimes. That is, if one can possibly justify the very long list of tenuous assumptions needed to make ecosystem models work.

The relatively simple framework provided by Ecopath and Ecosim readily incorporated several different fisheries, single-species model estimates of biomass and fishing mortality rates, abundance indices and catch data, and general biological information. Although more research into the parameterization, data requirements, and assumptions of the model must be done, the CNP Ecosim model offers alternative insights into the impacts of fishing on tuna and billfish dynamics, as well as potential indirect effects on their prey resources. Therefore, the approach may ultimately prove to be useful in the debate over the trade-offs and interactions among fisheries operating in the Pacific (FAO 1994).

Acknowledgments

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Bayesian mark–recapture estimation with an application to a salmonid smolt population

Samu Mäntyniemi and Atso Romakkaniemi

Abstract: We developed a Bayesian probability model for mark–recapture data. Three alternative versions of the model were applied to two sets of data on the abundance of migrating Atlantic salmon (*Salmo salar*) smolt populations, and the results were then compared with those of two widely used maximum likelihood models (Petersen method and a model using stratified data). Our model follows the basic principles of stochastic models presented for stratified data. In contrast to the earlier models, our model can deal with sparse data. Moreover, even weak dependencies between the studied parameters and the possible factors affecting them can be used to improve the plausibility of the estimates. The assumptions behind our approach are more realistic than those of earlier models, taking into account such factors as overdispersion, which is expected to be present in the mark–recapture data of salmon smolts because of their schooling behavior. Our examples also show that assumptions about the model structure can have a substantial impact on the resulting inferences on the size of the smolt run, especially in terms of the precision of the estimate.

Résumé : Nous avons mis au point un modèle de probabilité bayésien pour étudier des données de marquage et de recapture. Trois versions différentes du modèle ont été appliquées à deux séries de données sur l'abondance de populations de saumoneaux du saumon de l'Atlantique en migration et les résultats ont été comparés à ceux de deux modèles courants de vraisemblance maximale, la méthode de Petersen et un modèle qui utilise des données stratifiées. Contrairement à ces modèles plus anciens, le nôtre peut utiliser des données éparses. De plus, même des liens faibles entre les paramètres étudiés et les facteurs qui les affectent peuvent servir à augmenter la plausibilité des estimations. Les présuppositions sous-jacentes à notre méthodologie sont plus réalistes que celles des modèles précédents, car elles tiennent compte de facteurs tels que la surdispersion que l'on s'attend à trouver dans les données de marquage-recapture de saumoneaux à cause de leur comportement de nage en bancs. Nos exemples montrent aussi que les présuppositions faites au sujet de la structure du modèle peuvent avoir un impact important sur la taille estimée de la population migratrice de saumoneaux, particulièrement en ce qui a trait à la précision de l'estimation.

[Traduit par la Rédaction]

Introduction

Mark–recapture methods are widely used in the assessment of animal abundance (Otis et al. 1978; Seber 1982; Schwarz and Seber 1999). The simplest version of mark–recapture models is the Petersen method (Seber 1982), which assumes a closed population and equal recapture probabilities of all animals during the experiment. The Petersen method is an example of an easy method, but unfortunately it is also too simplistic to be genuinely useful in real applications. Methods with more realistic assumptions are required to analyze complex mark–recapture data. Considerable progress has already been made in developing models that are able to deal with, for example, catchability varying over time (Schwarz and Seber 1999). However, this development has been largely carried out in the context of maximum likelihood estimation. Bayesian mark–recapture models have also been developed (Castledine 1981; Gazey and Staley 1986; George and Robert 1992), but they too rely on the simplistic assumptions of, for example, independently behaving individuals.

Typical mark–recapture studies on migratory fish species like salmon aim to estimate abundance by partial trapping of either young fish leaving the nursery grounds for the feeding grounds or adult fish assembling in the spawning grounds following the feeding migration. In many such studies, capture probabilities have been reported to vary over the trapping period (Dempson and Stansbury 1991; Schwarz and Dempson 1994; Thedinga et al. 1994). In addition, smolts of Atlantic salmon (*Salmo salar*) have a tendency to school during their downstream migration (Kalleberg 1958; Bakshtanskiy et al. 1988; Fängstam et al. 1993), similar to smolts of Pacific salmon species (Burgner 1991; Heard 1991; Salo 1991). Social interaction between smolts has been suggested as the reason behind the schooling behavior (Allen 1944; Hansen and Jonsson 1985; Hvidsten et al. 1995). Schooling

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causes more variation in capture data (overdispersion) than there would be if smolts moved independently. Hvidsten et al. (1995) reported great overdispersion among daily smolt catches in the River Orkla, Norway. To date, implications of schooling behavior have not been taken into account in smolt abundance analyses.

In this paper we present a Bayesian probability model that can be used to derive the posterior probability distribution of the population size from stratified mark–recapture data. We combine the advantages of Bayesian modeling with the detailed statistical model presented by Schwarz and Dempson (1994). By considering the possibility of schooling behavior, a step towards more realistic model assumptions is taken. We also provide an option to incorporate into the model environmental covariates that might influence the values of estimated parameters. We analyze two data sets from Atlantic salmon smolt studies as examples: the Conne River data from Canada, presented and analyzed by Schwarz and Dempson (1994), and similar data from a much larger river in Scandinavia, the River Tornionjoki. Although we apply our model to the abundance estimation of Atlantic salmon, the model could be adapted to apply to any other animal species when using stratified mark–recapture data. The presence of dependent behavior in a form of, for example, spatial aggregation is typical among a wide range of animal species. Similarly, varying capture probability and its crucial role in the estimation of abundance are well recognized in the literature. Thus, our model has the potential to be applied to a wide range of biological problems.

Related study design

The model presented here is tailored to fit a common type of study design in partial smolt trapping. The basic idea is to provide continuous input of marked smolts upstream from the trap. Monitoring the recaptures of marked smolts provides information on the catchability of smolts. By having information on the catchability and knowing the number of unmarked smolts caught, it is possible to make inferences about the total number of smolts that passed the trapping site during the trapping period. It is assumed that there is at least one trapping device used continuously over the migration period. If two devices are available, the upper trap is used for marking and releasing with group-specific or individual marks and the lower "main trap" is used to catch both marked and unmarked smolts. If only one device is used, smolts that are caught are regularly marked and transported upstream and released for possible recapture. Here, the two-trap study design is represented by the Conne River and the one-trap design by the River Tornionjoki data. By assuming that the transportation of marked smolts corresponds to the use of a marking trap, the same model can be used in both cases.

Data from a study design described above is naturally temporally stratified. A proper unit of a stratum is 1 day, which can be easily justified by the commonly observed diurnal periodicity in the migration activity among Atlantic salmon smolts (Österdahl 1969; Hesthagen and Garnas 1986; Fängstam et al. 1993).

The following types of data are collected using the design described above. We release m_i smolts marked by individual or group-specific marks in day i. In each trapping day j, the number of smolts ($r_{i,j}$) recaptured in day j and released in day i is recorded, as well as the number (c_j) of unmarked smolts captured. Daily measurements of environmental covariates such as water level (WL_j) and water temperature (WT_j) can be recorded and used in the analysis. The notation for data and model parameters is summarized in Table 1.

Statistical methods

In this section, we present three Bayesian models for smolt trapping data. Because the Bayesian approach may be unfamiliar to some of the readers, we briefly explain the basic concepts of Bayesian inference (e.g., O'Hagan 1994) as they appear.

Models

We transfer two models from the frequentist framework to the Bayesian framework by using the original type of model structure, but completing the probability model by assigning prior distributions for model parameters. First, we formulate model M_P, a Bayesian version of the traditional Petersen model. The Petersen model is used here as a simple example to illustrate the notation and basic concepts of Bayesian modeling. The second model, M_{SD}, is based on the mark–recapture model introduced by Schwarz and Dempson (1994). However, the model is also improved by constructing a hierarchical structure for the model parameters. Finally, to allow for dependent behavior of smolts, we introduce model M_S, which accounts for overdispersion.

In each of the three models, it is assumed that (*i*) all marked and unmarked smolts migrate downstream, (*ii*) there is no mark loss between release and recapture sites, (*iii*) there is no mortality between release and recapture sites, (*iv*) the catchability of a marked smolt does not depend on the time spent in the river after release, and (*v*) marked and unmarked smolts have equal catchability and equal aggregation patterns.

Model M_P

In addition to assumptions *i*–*v*, the Petersen method is based on the assumption that all smolts move independently and are equally catchable throughout the whole trapping period. Thus, the total number of unmarked smolts caught ($C = \sum_{i=1}^{M} c_i$) is binomially distributed given the size of the unmarked population (U) and the catchability (q). By assumption *v*, the total number of recaptured smolts ($R = \sum_{i=1}^{M}\sum_{j=1}^{M} r_{i,j}$) is also conditionally binomially distributed given the total number of marked smolts released ($T = \sum_{i=1}^{M} m_i$) and the common catchability (q). Formally, the model specification is

$$(1) \qquad C|U, q \sim \text{Bin}(U, q)$$

$$R|T, q \sim \text{Bin}(T, q)$$

This model describes the stochastic relationship between the data and the model parameters and also completely defines the likelihood function of data.

The dependence structure of the model can be illustrated in terms of a directed acyclic graph (DAG; Fig 1*a*). A DAG

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Table 1. List of symbols used in the model specification.

Indices	
M	the number of recapture and release days
i	the day of release $i = 1,\ldots,M$
j	the day of recapture $j = i,\ldots,M$
Data (X)	
m_i	the number of smolts with group-specific marks released in day i
$r_{i,j}$	the number of smolts with group-specific marks released in day i and recaptured in day j
WT_j	the water temperature in day j
WL_j	the water level or the discharge in day j
c_j	the number of unmarked smolts captured in day j
Parameters (Θ)	
q_j	the catchability of smolts that pass the trapping site in day j
η_j	the mean of logit(catchability) in day j
ν_0, ν_1, ν_2	the intercept and regression coefficients of environmental covariates of logit(catchability)
λ_i	the random effect mean of log(traveling time) of a smolt group released in day i
ϕ_i	the random standard deviation of log(traveling time) of a smolt group released in day i
δ_i	the mean of random effects mean of log(traveling time) of smolts groups released in day i
ψ_0, ψ_1, ψ_2	the intercept and regression coefficients of environmental covariates of δ_i
π	the standard deviation of random means of log(traveling time) of smolt groups
γ_i	the mean of random standard deviations of log(traveling time) of smolt groups released in day i
ω_0, ω_1, ω_2	the intercept and regression coefficients of environmental covariates of $\log(\gamma_i)$
ρ	the standard deviation of random standard deviations
U	the size of the total smolt run
p_j	the probability that a smolt passes the trapping site in day j
u_j	the number of unmarked smolts passing the trapping site in day j
σ	the dispersion parameter of a beta-binomial distribution
ξ	the between-day standard deviation of catchability

is a graphical presentation of a statistical model that facilitates the understanding of the model structure. In a DAG, constants are denoted by rectangles and random variables by ovals. Dependencies between quantities are expressed by arrows: if parameter A follows a distribution with parameter B, there is a solid arrow that points from B to A. If parameter A is a function of parameter B, there is a broken arrow pointing from B to A. Frames or "plates" around a set of parameters are used to represent repetitive parts of the model. More detailed descriptions of DAGs in the context of fisheries science are given by, for example, Meyer and Millar (1999) and Wyatt (2002).

From a Bayesian point of view, the model specification is not yet complete. The idea of Bayesian modeling is to construct a full probability distribution for all quantities in the model, including both data and parameters. Equation 1 already defines the conditional distributions of the data given the parameters. A full probability model is completed by assigning prior probability distributions (priors) for the model parameters, in this case, to the catchability (q) and the total number of unmarked smolts (U). The prior should represent the uncertainty, in the form of probability statements, about the parameter values before obtaining any data. In this regard, the Bayesian approach to inference is very different from the frequentist one. In particular, the frequentist approach does not allow us to make probability statements about parameter values. The prior distributions can be based on previous measurements of the population size and catchability, physical properties of the area occupied by the population, properties of the sampling design, etc. Thus the prior distribution should always depend on the context. With the notation $U \sim D()$, $q \sim D()$, we express that prior distributions are assigned to these parameters.

Sometimes it may be justified to ignore even strong prior information to see what the value of the data is alone. According to Raftery (1988), a vague prior distribution for the population size in a binomial experiment would be proportional to $1/U$. A vague prior for the catchability is a uniform distribution between 0 and 1.

Model $\mathbf{M}_{SD}$

Here we present a Bayesian version of the model introduced by Schwarz and Dempson (1994). In addition to assumptions *i*–*v*, Schwarz and Dempson (1994) assumed that smolts move independently and that the catchability of smolts remains constant within each day. However, they allowed the catchability to vary between days. The basic idea of their model to allow for variable catchability is to perform Petersen estimations separately for each day. This requires that the movement of each release group be modeled to assess the probability of a marked smolt passing the trap in day j. The distribution for the daily catches is then

$$(2) \qquad c_j | u_j, q_j \sim \mathrm{Bin}(u_j, q_j)$$

$$r_{i,j} | q_j, \theta_{i,j}, m_i \sim \mathrm{Bin}(m_i, q_j \theta_{i,j})$$

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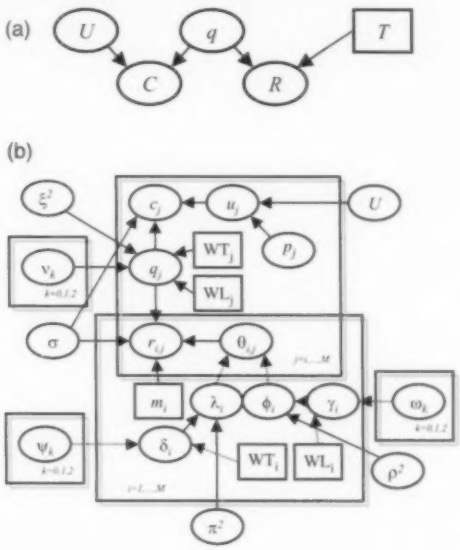
Fig. 1. Directed acyclic graphs (DAG) for (*a*) model M_P and (*b*) model M_S. The DAG for model M_{SD} is similar to that for M_S, but it does not contain parameter σ. Model M_P assumes constant catchability over time and independent behavior of individuals, model M_{SD} assumes temporally varying catchability and independent behavior, and model M_S assumes temporally varying catchability and schooling behavior.



where $\theta_{i,j}$ is the probability that a smolt released on day i will pass the trap on day j. Thus, probabilities $\theta_{i,1},\ldots,\theta_{i,M}$ describe the movement of the group of smolts released on day i. Following the idea of Schwarz and Dempson (1994), the movement of a release group is modeled by a log-normal distribution from which the probabilities $\theta_{i,j}$ are calculated as

$$\theta_{i,j} = \Phi\left(\frac{\log(j-i+0.5)-\lambda_i}{\phi_i}\right) - I_{i,j}\Phi\left(\frac{\log(j-i-0.5)-\lambda_i}{\phi_i}\right) \quad (3)$$

where $I_{i,j} = 1$ if $j > i$ and 0 otherwise, λ_i is the mean of log(traveling time) of smolts released on day i, ϕ_i is the standard deviation of the log(traveling time) of smolt group released on day i, and Φ denotes the cumulative density function of the standard normal distribution.

Schwarz and Dempson (1994) assumed that the catchabilities (q_j) were independent, i.e., learning, for example, about the catchability in day $j = 5$ contains no information about the catchability in other days (q_j, $j \neq 5$). Similar assumptions of independence were also made about movement parameters (λ_i, ϕ_i). If such a model seems reasonable, independent prior distributions should be assigned to each catchability and movement parameter.

Our approach is to assume that the daily catchabilities are only conditionally independent, that is, we assume that daily catchabilities vary between days according to a distribution. The parameters of this distribution are not known, but the data are used to learn about the parameters. Observing data from days $j = 2,\ldots,M$, for example, makes it possible to learn about the between-day mean and variance of the catchability. The information can be used to draw inferences about the catchability in day 1 even without using the data observed in that day. This kind of information transfer can be formally built into the model by assuming that daily catchabilities form an independent sample from a distribution of catchabilities, which then has an unknown mean and variance. Modeling parameters of the data by another set of parameters (which are often called hyperparameters) is referred to as hierarchical modeling. Advantages and properties of hierarchical modeling in stock assessment are presented in more detail by Wyatt (2002).

Here we assume that the logit-transformed catchabilities ($\log(q_j/(1-q_j))$) form an independent sample from the Normal distribution with unknown mean (η_j) and variance (ξ^2):

$$\log(q_j/(1-q_j))|\eta_j,\xi^2 \sim N(\eta_j,\xi^2) \quad (4)$$

$$\eta_j = \nu_0 + \nu_1 WT_j + \nu_2 WL_j$$

$$\nu_0 \sim D(),\ \nu_1 \sim D(),\ \nu_2 \sim D(),\ \xi^2 \sim D()$$

The mean is assumed to be a function of environmental covariates with regression coefficients ν_0, ν_1, and ν_2. Here, the considered environmental covariates are water temperature (WT_j) and water level or water discharge (WL_j). Hierarchical modeling is useful also when modeling the movement of release groups. It should be reasonable to assume that the mean traveling time (e^{λ_i}) from the release site to the trapping site is not equal for all release groups. However, it is also plausible to think that learning about the mean traveling time from a subset of days would provide us with information about the mean traveling time in the remaining days. A similar reasoning also holds for the standard deviation of the log(traveling time) (ϕ_i). These ideas can be formally modeled in the same way as the catchability:

$$\log(\phi_i)|\gamma_i,\rho^2 \sim N(\gamma_i,\rho^2) \quad (5)$$

$$\gamma_i = \omega_0 + \omega_1 WT_i + \omega_2 WL_i$$

$$\omega_0 \sim D(),\omega_1 \sim D(),\omega_2 \sim D(),\rho^2 \sim D()$$

$$\lambda_i|\delta_i,\pi^2 \sim N(\delta_i,\pi^2) \quad (6)$$

$$\delta_i = \psi_0 + \psi_1 WT_i + \psi_2 WL_i$$

$$\psi_0 \sim D(),\psi_1 \sim D(),\psi_2 \sim D(),\pi^2 \sim D()$$

Now we have a flexible model for the movement of each release group. Environmental covariates are allowed to influence the expected values of movement parameters, but also the possibility of unexplained random variation is taken into account by measuring the between-day variation by variances ρ^2 and π^2.

To make the assessment of the prior distributions of daily run sizes (u_j) easier, we construct the prior in two phases. First, a prior distribution is assigned to the total size of the population (U) that passes the trapping site during the M days of trapping. Then the probability (p_j) that a smolt from this population would pass the sampling site in day j should be assessed. Obviously, it is necessary that $\sum_{j=1}^{M} p_j = 1$. This condition is satisfied by assigning a Dirichlet prior for

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the vector of probabilities. Given that there are U smolts that distribute to M days according to the probabilities $(p_1,\ldots,p_M)$, the daily run sizes $(u_1,\ldots,u_M)$ are multinomially distributed:

$$(7)\quad (u_1,\ldots,u_M)|U,(p_1,\ldots,p_M) \sim \text{Multin}(U,(p_1,\ldots,p_M))$$
$$(p_1,\ldots,p_M)|(a_1,\ldots,a_M) \sim \text{Dirichlet}((a_1,\ldots,a_M))$$
$$U \sim D()$$

where $(a_1,\ldots,a_M)$ is a vector of constants that must be given by the user to represent prior beliefs about the run curve. The expectation of p_j is $a_j/\sum_{j=1}^{M} a_j$ and the variance increases as $\sum_{j=1}^{M} a_j$ decreases. The vector $(a_1,\ldots,a_M)$ can also be interpreted to represent a prior experiment with $\sum_{j=1}^{M} a_j$ individuals from which a_j individuals passed the trapping site in day j.

Equations 2–7 now define the full probability model for the mark–recapture data and model parameters. The model has more parameters than there are data points. However, the structural assumptions made about the dependencies between parameters makes it possible to obtain information about parameter values from data.

Model $\mathbf{M_S}$

In model M_{SD}, the assumption of independently moving smolts gave rise to the assumption that the catches $(c_j, r_{i,j})$ of smolts would be binomially distributed given the movement parameters, catchability, and population size (eq. 2). However, when smolts migrate in schools, they clearly are not behaving independently. Because of this, binomial distribution may be too tightly concentrated to properly describe the behavior of the catches. It is more appropriate to use a distribution that is overdispersed with respect to the binomial distribution, because when smolts move in groups, it is more likely to observe higher or lower catches than predicted by a binomial distribution (Fig. 2). Our choice is to substitute the binomial distribution by one of its overdispersed alternatives, the beta-binomial distribution (Gelman et al. 1995). Thus, to modify the model M_{SD} to model M_S, which allows for overdispersion in catches, we substitute eq. 2 by the specification

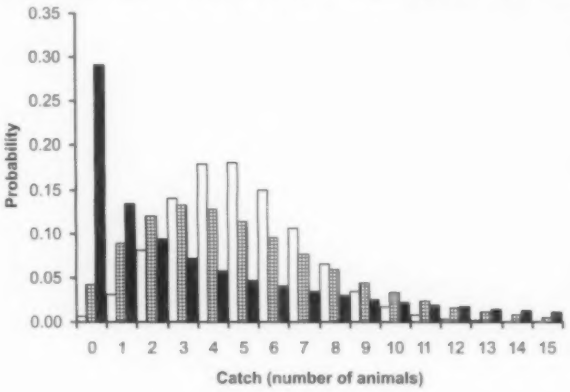
$$(8)\quad c_j|u_j, q_j, \sigma \sim \text{Beta-bin}(u_j, q_j, \sigma)$$
$$r_{i,j}|m_i, q_j, \theta_{i,j}, \sigma_r \sim \text{Beta-bin}(m_i, q_j\theta_{i,j}, \sigma_r),$$
$$\sigma_r = (\sigma+1)\frac{(1-q_j\theta_{i,j})}{\theta_{i,j}(1-q_j)} - 1$$

where σ is the dispersion parameter, assumed to be equal over the whole trapping period and equal for all smolt groups. The role of σ is to adjust the dispersion of the distribution of the catches. If σ is close to 0, there is very much overdispersion, and when σ approaches infinity, the limiting distribution is binomial (Fig. 2). We use a beta-binomial density of the form

$$(9)\quad p(r|q,\sigma,u) = \frac{\Gamma(u+1)}{\Gamma(r+1)\Gamma(u-r+1)} \times \frac{\Gamma(q\sigma+r)\Gamma(u+(1-q)\sigma-r)}{\Gamma(\sigma+u)} \times \frac{\Gamma(\sigma)}{\Gamma(\sigma q)\Gamma(\sigma(1-q))}$$

where Γ denotes the Gamma function. After a positive-valued prior distribution is selected for σ, model M_S (eqs. 3–8) is completely defined.

Fig. 2. Probability distributions of recaptures in three situations where the number of released animals (u) is 100 and the catchability (q) is 0.05. Independent behavior corresponds to binomial distribution (open bars), and the effect of schooling behavior is represented by beta-binomial distributions with dispersion parameters σ = 10 (solid bars) and σ = 70 (hatched bars).



Parameter estimation

In the Bayesian approach, parameter estimation is a procedure of updating the prior distribution $p(\Theta)$ of parameters Θ, which describes the uncertainty about the parameter values prior to seeing the data, to the posterior distribution $p(\Theta|X)$, which describes the uncertainty about the parameter values after seeing the data. This is accomplished by an application of Bayes' theorem, which combines the information contained in the data via the likelihood function $p(X|\Theta)$ with the prior $p(\Theta)$.

$$(10)\quad p(\Theta|X) = \frac{p(X|\Theta)p(\Theta)}{\int p(X|\Theta)p(\Theta)d\Theta} \propto p(X|\Theta)p(\Theta)$$

The formula of the posterior distribution is often so complex that analytical calculations are impossible in practice. However, samples from the posterior distribution can usually be obtained by using Markov chain Monte Carlo (MCMC) simulation (Gilks et al. 1995). After obtaining a very large sample from the posterior distribution, the histogram of samples is used as an approximation.

WinBUGS (Spiegelhalter et al. 1995) is a software package that makes the implementation of MCMC simulation easy. WinBUGS requires the model specification in a form of conditional distributions written in WinBUGS language. The use of WinBUGS and MCMC in the context of fisheries

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science have been discussed in more detail by Meyer and Millar (1999) and Millar and Meyer (2000).

Examples

To compare our approach with earlier methods and to illustrate the effects of different assumptions on the resulting posterior distributions, we analyzed two data sets as examples of model fitting. We reanalyzed the data provided by Schwarz and Dempson (1994) describing an Atlantic salmon smolt population in the Conne River, Newfoundland, Canada. Our second source of data is the trapping of Atlantic salmon smolts in the River Tornionjoki in northern Scandinavia.

We fitted four models to both data sets. Models M_P, M_{SD}, and M_S were fitted as they appear in the previous section. In addition, we fitted a restricted version of M_S that did not utilize any environmental covariates ($\nu_1 = \nu_2 = \omega_1 = \omega_2 = \psi_1 = \psi_2 = 0$). This model is denoted by M_S^r.

For the analyses, we assigned vague priors for the model parameters. To obtain a uniform prior density for catchabilities q_j, the prior distributions of the coefficients ν_0, ν_1, and ν_2 of the regression model (eq. 4) were set to be $N(0,0.5)$ and the inverse of the random variance ξ^2 was assigned a Gamma(1,1) prior density. Diffuse prior distributions were assigned to the other hyperparameters of the models. The prior density of the size of the total smolt run U was assumed to be proportional to $1/U$ in the range between 1 and 5 000 000 smolts for both rivers. WinBUGS 1.3 MCMC software (Spiegelhalter et al. 1995) was used to draw large samples from the posterior distributions of model parameters (WinBUGS code is available from authors upon request). MCMC simulation was carried out until Monte Carlo (MC) errors of all parameters were less than 5% of the posterior standard deviation. MC error is the standard error of the mean of the MCMC samples (Gilks et al. 1995), and it can be made arbitrarily small by increasing the number of samples from the posterior distribution.

Conne River

The Conne River is 193 km long with a drainage area of 602 km^2 (Dempson and Stansbury 1991). Salmon smolts were caught in 1987 by two counting fences and were marked with streamer-tags at the upper trap to be recaptured at the lower trap. The study area, study design, and trapping methodology have been described in detail by Dempson and Stansbury (1991) and Schwarz and Dempson (1994).

The random variation in movement parameters between release groups was lower in model M_S than in model M_{SD}: the posterior means of ρ^2 and π^2 were reduced from 0.20 and 0.14 (M_{SD}), respectively, to 0.18 and 0.10 (M_S). The posterior mean of between-day variation in the catchability (ξ^2) was also reduced from 0.78 (M_{SD}) to 0.28 (M_S). This suggests that when overdispersion of catches is not allowed, the model explains the extra variation in catches by random variation in the movement parameters and by between-day variation in the catchability.

According to the model M_S, the data suggest that there are associations between environmental covariates and model parameters: the catchability was positively associated with water discharge ($P(\nu_1 > 0) \approx 1.00$) and water temperature ($P(\nu_2 > 0) \approx 1.00$). The mean of the traveling time distribution was not very clearly related to the discharge ($P(\psi_1 > 0) \approx 0.48$) but was negatively associated with the water temperature ($P(\psi_2 < 0) \approx 0.99$). The standard deviations of the traveling time distributions were not clearly related to environmental covariates ($P(\omega_1 > 0) \approx 0.75$, $P(\omega_2 > 0) \approx 0.70$).

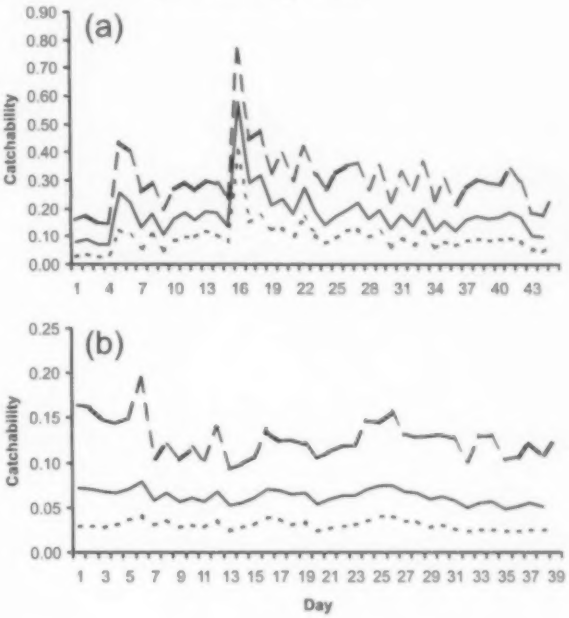

Fig. 3. Trajectories of 2.5% (dotted line), 50% (solid line), and 97.5% (broken line) percentiles of the posterior distributions of the catchability (q) in (*a*) the Conne River and (*b*) the River Tornionjoki from model M_S. Model M_S assumes temporally varying catchability and schooling behavior.

Including environmental covariates seemed to reduce the between-day random variation in the model parameters and also the amount of overdispersion. The clearest reduction (from 0.19 in model M_S^r to 0.10 in model M_S) took place in the posterior mean of π^2, which describes the random variation in mean traveling times between release groups. Correspondingly, the posterior mean of ξ^2 was reduced from 0.37 to 0.28. The amount of overdispersion also decreased when environmental covariates were used. This can be seen from the posterior means of σ from models M_S (22.12) and M_S^r (11.84) of which model M_S^r does not use environmental covariates. According to model M_S, the posterior median of the catchability varies from 0.1 to 0.6 because of random variation and environmental covariates (Fig. 3*a*).

The models M_{SD}, M_S, and M_S^r produced substantially different posterior distributions for the size of the total smolt run (Fig. 4*a*). From these, model M_{SD} produced the most concentrated posterior distribution. The Bayesian Petersen model (M_P) produced an even more concentrated posterior distribution than model M_{SD} (Table 2). Although frequentist confidence intervals and Bayesian posterior probability intervals are conceptually very different, their comparison is

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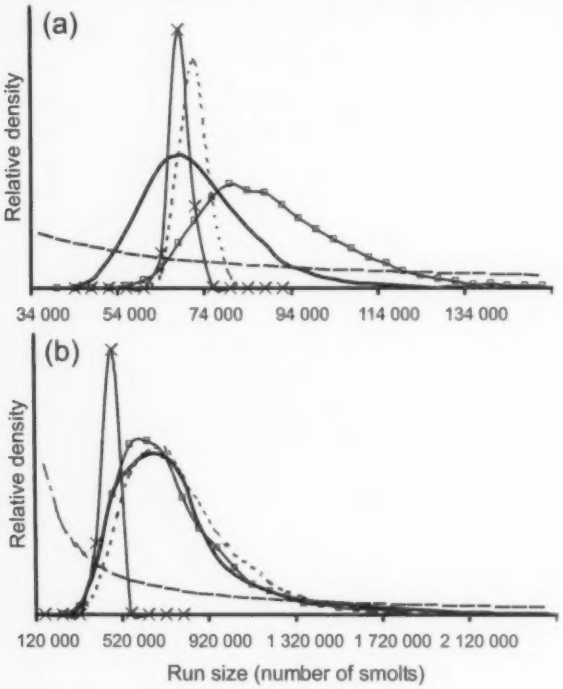
Fig. 4. Posterior distributions of the total run size in (*a*) the Conne River 1987 and (*b*) the River Tornionjoki 2001 from the models M_S (solid line), M_{SD} (dotted line), M_S^r (solid line with open squares), and M_P (solid line with crosses). Broken line represents the prior distribution. Densities have different scales for the sake of illustration. Model M_P assumes constant catchability over time and independent behavior of individuals, model M_{SD} assumes temporally varying catchability and independent behavior, and model M_S assumes temporally varying catchability and schooling behavior. Model M_S^r is extracted from model M_S by excluding the use of environmental covariates.



nevertheless interesting. The Bayesian version of the model developed by Schwarz and Dempson (1994) yielded a narrower interval than the original maximum likelihood model. There is also the difference that the original analysis of Schwarz and Dempson (1994) used the Petersen method for the first and for the last part of the run, whereas the Bayesian version (M_{SD}) used the same model for the whole data set.

The choice of the model seems to play a major role in the inference about the smolt run in the Conne River in 1987. Because there is firm evidence that smolts form schools during their migration and because we believe that environmental conditions can affect the behavior of smolts and the trapping success, we consider model M_S to be the most plausible from among the models presented here for the Conne River smolt trapping.

In addition, model M_S provided some information about the behavior of smolts: when water temperature rose, marked smolts tended to speed up their migration. They were also easier to catch when the water was warm and the discharge was high. However, these associations may not be causal, because there may be latent factors affecting such observed phenomena. The use of environmental covariates reduced the amount of overdispersion, and thus the coefficient of variation (CV) of the posterior of the total smolt run was reduced by about 10% from model M_S^r to model M_S.

River Tornionjoki

The River Tornionjoki, which flows into the northern end of the Baltic Sea, and its headwaters form a 500 km long border between northern Finland and Sweden. It is the largest, with a drainage area of approximately 40 000 km^2, and most productive of the Baltic salmon rivers. The annual mean discharge is about 380 m^3·s^{-1}, and during the spring flood (May – early July), when smolts migrate out from the river, the discharge is commonly 1000–2000 m^3·s^{-1} at the trapping site near the river mouth.

In the River Tornionjoki, only a single large trap was used because of logistical problems. Usually the smolt trap was emptied once a day, but during the peak run, this was done more frequently. Daily, smolts were marked by streamer-tags and were immediately transported upstream to a release site. The smolt trapping data (Table 3) from the summer of 2001 is clearly more sparse than the data used by Schwarz and Dempson (1994).

According to the results from model M_S, environmental covariates and model parameters had some associations. The mean traveling time was clearly negatively related to water temperature ($P(\psi_2 < 0) \approx 1$) and positively related to water level ($P(\psi_1 > 0) \approx 0.98$). The other model parameters were not that clearly associated with environmental covariates ($P(\nu_1 > 0) \approx 0.69$, $P(\nu_2 > 0) \approx 0.36$, $P(\omega_1 > 0) \approx 0.21$, and $P(\omega_2 > 0) \approx 0.21$). Catchability did not seem to vary very much during the trapping period (Fig. 3*b*). Model M_S yielded a posterior mode at 650 000 smolts and a standard deviation of 363 000. The posterior distributions from models M_{SD} and M_S^r were very close to that obtained from model M_S. However, their standard deviations were slightly smaller, apparently because of the heavier tail of the posterior distribution obtained from model M_S (Fig. 4*b*).

Again, from a biological perspective, we consider model M_S to be the most plausible of these four alternatives. However, in the case of the River Tornionjoki in 2001, the selection between models M_S, M_S^r, and M_{SD} does not substantially change the inferences that can be made about the size of the smolt run. In contrast to these, model M_P yields posterior mode at 418 000 smolts and a standard deviation of 22 700.

Discussion

Properties of the models

Using the idea of hierarchical modeling removes the problem of small sample size often faced in the frequentist framework. For example, Schwarz and Dempson (1994) did not include the first and the last days of the smolt trapping period in their detailed analysis because of sparse data. They also assumed that the daily catchabilities were independent and that movement parameters of each release group of smolts are independent of the movement parameters of the other release groups. Our approach utilizes the hierarchical structure in model parameters, which makes it possible to apply the model over the entire trapping period, with days borrowing information from each other. This is a general feature of hi-

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Table 2. Run size estimates for the Conne River smolt population in 1987 produced by different models together with the maximum likelihood (ML) estimates provided by Schwarz and Dempson (1994).

Bayesian models	Mean	Mode	SD	2.5%	97.5%	CV
M^r_S	88 700	78 000	18 000	63 000	130 000	0.20
M_S	70 500	67 000	12 800	50 400	101 000	0.18
M_{SD}	69 500	69 000	3 000	63 700	75 800	0.04
M_P	66 500	66 500	1 930	62 900	70 500	0.03
ML models		MLE	SE	95% confidence interval		
Schwarz and Dempson		69 609	3 565	62 500 – 76 740		
Petersen		67 250	2 159	62 942 – 71 578		

Note: CV, coefficient of variation; SD, standard deviation; SE, standard error.

erarchical Bayes models, known as "shrinkage" (O'Hagan 1994): parameter estimates from days with sparse data are pulled towards the common mean. As a consequence, there will be no need to judge afterwards which parameter estimates are to be used in the calculations or to use interpolation to find "better" estimates.

Uncertainty included in the posterior distribution of population size is heavily dependent on assumptions made about the behavior of animals. Salmon smolts in natural conditions are typically not independent because of their tendency to form schools during migration. Hence, methods that assume independent behavior appear far too optimistic about the precision of the estimation procedure. Our models M_S and M^r_S take into account this additional uncertainty by allowing for overdispersion in recapture data. They also take into account other possible latent factors affecting catchability by allowing for random variation in the daily catchabilities.

As shown by the example from the Conne River, allowing for overdispersion may also have an impact on point estimates of the population size. This is likely to happen when catchability is low and the amount of overdispersion is high. By allowing for overdispersion, we allow the probability that large schools of animals pass the trapping without getting caught to increase. If overdispersion gets support from the observed data, the mode of the posterior distribution of the population size will support larger population sizes than in the case of independent behavior. However, assumptions about the temporal variation in catchability also play a role in this comparison, because the posterior distribution of the population size is sensitive to daily variation in catchability during the days with high catches of unmarked animals.

As demonstrated in methodological literature (e.g., O'Hagan 1994; Gelman et al. 1995) and also here, the Bayesian framework allows for explicit incorporation of prior knowledge. In our examples, there may be substantial prior knowledge about behavior and movement of the smolts, size and distribution of the smolt population, and possible effects of environmental factors on sampling or smolt migration.

One more key point in using the Bayesian framework is that the end product of the analysis is a probability distribution of the population size, which is useful when making management decisions under rigorous assessment of uncertainty (McAllister and Kirkwood 1998; Wade 2000).

Model selection

Our view is that the model selection for mark–recapture data should be based primarily on the plausibility of a model. That is, one should make sure that the assumptions of the model correspond, as well as possible, to substantive biological knowledge about the animal behavior and about the properties of the study design. Formal model selection procedures are useful only when comparing models that are equally plausible from a biological perspective. Formal methods of model selection and model averaging, like the ones proposed by King and Brooks (2001), would be useful when comparing different structural assumptions, for example, whether to use a probit-link function instead of a logit-link one in the regression equation of daily catchability.

The adequacy of the selected model can be assessed by comparing the posterior predictive distributions of the model with the observed data (Gelman et al. 1995). In the case of mark–recapture data, the interpretation of such model-checking results is not straightforward: most of the recaptures are zeros, which are easily predicted by almost any model. Because of the large number of zeros, most of the residuals are also very close to zero, making their interpretation very difficult. For these reasons, we have not included model-checking procedures in this work.

Violations in model assumptions

All mark–recapture models have basic assumptions that should be filled in the real world to achieve some credibility for the analysis. Our model M_S assumes that there is no mark loss or mortality of marked fish. To some extent, these assumptions can be empirically tested by monitoring marked fish in captivity.

Another important assumption made in all mark–recapture models is that marked individuals should have catchability equal to that of unmarked individuals. In the case of aggregating species, marked and unmarked individuals should also show similar aggregation patterns. However, marked individuals are allowed to move at different speeds than unmarked individuals, because only the schooling behavior of fish when passing the trap matters in the estimation of the population size. Violation of the assumption of equal catchability has different consequences depending on whether the marked individuals exhibit trap shyness or trap happiness.

Consequences of violation of model assumptions are basically similar in both the Bayesian and the frequentist frameworks. In the context of mark–recapture of smolts, for example, Dempson and Stansbury (1991) have treated the subject. If there existed knowledge about violation of the model assumptions, the Bayesian framework would allow flexible ways to incorporate quantitative correction of these sources of errors. For instance, one could introduce a parameter representing the difference in the catchability of marked

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Table 3. The data from the smolt trapping experiment in the River Tornionjoki, 2001.

Date	*m*	Recoveries by number of days following release														*c*	WT, °C	WL, 0.1 m
		1	2	3	4	—	7	—	13	—	15	—	17	—	20	21			
28 May	79				2		1						1			1	83	6.21	10.00
29 May	26																27	5.96	10.00
30 May	9								1		1						9	6.48	9.60
31 May	77	1	1		1												83	7.70	8.70
1 June	136	29													1		143	9.00	7.90
2 June	60	3															227	10.40	6.90
3 June	182	9															355	11.23	6.30
4 June	138	4															146	11.52	5.60
5 June	169	11	1														176	11.07	5.00
6 June	33																60	10.74	4.90
7 June	41	9															78	11.81	5.20
8 June	73																285	12.14	5.30
9 June	79	1															169	12.64	5.80
10 June	242	9		1													708	13.27	5.90
11 June	251	24	1														815	12.98	6.50
12 June	286	7															3 810	12.53	8.00
13 June	152		3														6 847	12.74	10.40
14 June	393	8															2 212	12.90	11.90
15 June	205															na	1 345	13.67	13.00
16 June	223	3													na	na	413	14.09	13.70
17 June	218	3													na	na	324	14.66	13.80
18 June	418	17													na	na	571	15.27	13.40
19 June	464	56	1										na		na	na	642	15.41	13.00
20 June	485	36	1										na		na	na	583	15.75	12.80
21 June	177	27									na		na		na	na	2 061	16.19	12.60
22 June	189	19	1								na		na		na	na	1 405	16.33	12.05
23 June	137	9							na		na		na		na	na	631	17.34	11.10
24 June	0								na		na		na		na	na	163	18.18	10.60
25 June	160	15							na		na		na		na	na	241	18.91	9.20
26 June	0								na		na		na		na	na	255	19.50	8.20
27 June	66								na		na		na		na	na	221	20.03	7.50
28 June	0								na		na		na		na	na	129	19.92	6.90
29 June	0						na		na		na		na		na	na	56	19.94	6.20
30 June	44						na		na		na		na		na	na	52	19.86	5.70
1 July	20						na		na		na		na		na	na	22	19.88	5.05
2 July	0				na		na		na		na		na		na	na	7	19.58	4.90
3 July	0			na	na		na		na		na		na		na	na	7	18.81	4.45
4 July	0		na	na	na		na		na		na		na		na	na	2	18.75	4.15
5 July	0	na	na	na	na		na		na		na		na		na	na	10	19.31	4.10
Total	5232						314 Streamer-tagged smolts recaptured										25 373		

Note: Columns with no recaptures are omitted to save space. *m*, number of released smolts; *c*, number of unmarked smolts captured; WT, water temperature; WL, water level; na, not available; no entry, 0.

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and unmarked animals and express the knowledge about the difference in the form of a prior probability distribution.

Model modifications and future research

There are many variations and extensions of our model that may be of interest in ecological studies. For example, the population of interest may include distinguishable subgroups of animals, such as wild and hatchery-reared individuals among salmon smolts. Because subgroups with different histories may differ, for instance, in their behavior in relation to sampling procedures, it may be of interest to model the subgroups separately. For example, the means of the catchability and (or) movement distributions could differ across groups, whereas the other model parameters could remain equal.

In models M_{SD} and M_S, we assumed that daily catchabilities vary randomly between days, given that the mean and variance are known. However, it could also be justified to assume that the random deviations in catchabilities in successive days are correlated. This idea could be implemented by using an autoregressive structure in the prior distribution. This kind of assumption may improve the precision of posterior distributions for catchabilities and the precision of the posterior distribution of the total run size.

We assumed that the amount of overdispersion does not change during the experiment. This may not be appropriate in all cases, because animals may change their tendency to aggregate during the experiment. The aggregation pattern may also vary spatially, which is important to take into account when multiple recapture sites are used.

In our examples we used vague prior distributions of model parameters. In practice, prior information about various parameters might well exist. For example, prior information about the smolt run may be obtained from a probabilistic salmon parr population model, which uses the data from sampling of parr. If a mark–recapture experiment is performed according to a constant design in successive years, it is possible to obtain prior information about the relationship between environmental factors and model parameters. For example, the basic level of catchability may vary independently between years, but the regression slopes of environmental covariates might be quite similar each year. Meta-analysis of multiple years could also be used to learn about the shape of the run curve and its relationship with environmental factors like water temperature as a trigger of the smolt run. Hierarchical Bayesian meta-analysis of this kind could also be extended to cover mark–recapture studies in several distinct populations of an animal species. All of these diverse ways to incorporate prior information in the analysis will eventually result in reduced posterior uncertainty about the population size, provided that the prior information is not in strong disagreement with the information contained in the observed data.

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Larval sand lance (*Ammodytes* sp.) in the diet of small juvenile wolffish (*Anarhichas* spp.): predatory interactions in frontal water masses off western Greenland

Peter Munk

Abstract: The predatory behaviour of two species of juvenile wolffish (*Anarhichas lupus* and *Anarhichas minor*) was studied during a field campaign across a frontal area off western Greenland. The study focused on ontogenetic changes in prey-type and -size preference of the wolffish and their predatory impact on a cohabiting population of larval sand lance (*Ammodytes* sp.). Sampling took place along a cross-shelf transect at latitude 66°20′N, and the analysis is based on stomach contents of assembled wolffish (2–5 cm in length) and abundance estimates of plankton and fish. An ontogenetic change in wolffish prey preference was evident as a dietary shift from copepods and smaller amphipods to larger amphipods and fish larvae. The inclusion of fish larvae in the wolffish diet led to a marked increase in prey biomass, and fish larvae constituted up to 77% of diet biomass in the largest juveniles caught. Wolffish selectively targeted the smaller-sized part of the larval sand lance population; hence, larval vulnerability increased with decreasing size. Comparison between estimated predation rates and abundances of predator and prey indicated larval predation mortalities of up to 5% per day, with mortality peaking in the vicinity of a hydrographic front. Hence, findings suggest substantial predation pressure on larvae, primarily related to larval size and distribution.

Résumé : Le comportement de prédation de deux espèces de jeunes loups (*Anarhichas lupus* et *Anarhichas minor*) a été étudié de part et d'autre d'une région frontale lors d'une mission en mer au large de la côte occidentale du Groenland. L'étude a porté sur les changements ontogéniques dans les préférences de types et de tailles de proies chez les loups et les conséquences de cette prédation sur la population concomitante de larves de lançons (*Ammodytes* sp.). L'échantillonnage a été mené à travers la plate-forme suivant la latitude 66°20′N. L'analyse comprend une étude des contenus stomacaux de l'ensemble des loups (2–5 cm de longueur) et des estimations de l'abondance du plancton et des poissons. Il se produit une changement ontogénique dans les préférences alimentaires des loups, soit un déplacement alimentaire des copépodes et des petits amphipodes vers les amphipodes plus grands et les larves de poissons. L'addition de larves de poissons au régime alimentaire des loups augmente de façon appréciable la biomasse des proies et ces larves représentent jusqu'à 77 % de la biomasse alimentaire chez les plus grands des jeunes loups capturés. Les loups ciblent de façon sélective la fraction de plus petite taille de la population de larves de lançons et donc la vulnérabilité de ces larves diminue avec la taille. La comparaison des taux estimés de prédation et des abondances de prédateurs et de proies laisse voir que la mortalité des larves due à la prédation peut atteindre jusqu'à 5 % par jour et que cette mortalité est maximale près d'un front hydrographique. Ces résultats indiquent donc l'existence d'une importante pression de prédation sur les larves, en rapport principalement avec leur taille et leur répartition.

[Traduit par la Rédaction]

Introduction

Mortality is high during the early life of fish, and both indirect and direct evidence suggest that the major source of mortality can be predation, exerted by both invertebrate and vertebrate predators (Bailey and Houde 1989; Leggett and DeBlois 1994; Fortier and Villeneuve 1996). In regions where larvae of multiple species hatch over extended periods of time, larger larvae and juveniles have the potential to be significant predators of the smaller larvae. Experimental studies where larval and juvenile/adult fish are reared together in tanks or mesocosms often show heavy predation by the older fish (Fuiman and Gamble 1988; Monteleone and Houde 1992), but in the field the prey–predator interactions have been difficult to identify and describe. Field-based quantitative and qualitative descriptions of predation on fish larvae are limited by the scarcity of identifiable larval remains in the stomachs of potential predators. This is believed to be due to fast digestion of fish larvae; for example, 50% of captured cod larvae are unidentifiable after 15–90 min (5 mm larvae) or 2–3 h (15 mm larvae) in stomachs of cod juveniles (Folkvord 1993). Calculations by Folkvord (1993) show, however, that predation–cannibalism might be detected with a reasonable sampling effort, even at digestion rates of this magnitude. Accordingly, the occasional

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findings of significant numbers of larvae in stomachs of fish predators show that a fast digestion of larvae does not ultimately hinder their detection. Such findings of larvae in stomachs have predominantly been reported for predatory larvae/juveniles of the family Scrombidae (Peterson and Ausubel 1984; Sanchez-Velasco et al. 1999; Hillgruber and Kloppmann 2001). During these studies, the fish larvae often constitute more than 50% (by number) of the diet, with a tendency of increasing percentage with predator size.

Larval fish remains have also been found in significant quantities in the stomachs of small juveniles from the family of wolffishes (Anarhichadidae) (Falk-Petersen et al. 1990; Ortova et al. 1991). Three species of this family are widely distributed in the North Atlantic, Atlantic wolffish (*Anarhichas lupus*), spotted wolffish (*Anarhichas minor*), and northern wolffish (*Anarhichas denticulatus*). They are abundant in the areas off western Greenland, and larvae/juveniles of these species are commonly observed during a series of annual surveys covering the area (Pedersen and Smidt 2000). The wolffish distribution coincides with the larval distribution of a number of other fish species, of which the most abundant are the sand lance (*Ammodytes* sp.), American plaice (*Hippoglossoides platessoides*), and Greenland halibut (*Reinhardtius hippoglossoides*) (Pedersen and Smidt 2000). Because of the early spawning and larval emergence of wolffish (Templeman 1986), they are often larger than other young-of-the-year in the area and are potentially important predators of these.

An investigation on plankton dynamics and fish recruitment processes off western Greenland in July 2000 included a study of the predatory impact of juvenile wolffish on the larval fish populations in the area. The main aims were to describe the ontogenetic changes in predatory behaviour and the relative importance of fish larvae to wolffish diet and to evaluate the predation pressure exerted by the juvenile wolffish on the larval fish population. To accomplish this, the distributional overlap between larval and juvenile species was quantified by sampling along a cross-shelf transect, whereas the wolffish predation was investigated at a specific site of high abundances of both larvae and juveniles.

Materials and methods

Sampling was carried out along 66°20′N during 19–22 July 2000. The first two stations of the transect were situated offshelf, close to the 600-m isobath, and inshore of these another 10 stations were positioned at intervals of 5–10 nautical miles (Fig. 1). Sampling at each station was initiated by temperature and salinity measurements from surface to 5 m above bottom using a Seabird 9/11 CTD (conductivity–temperature–depth; Sea-Bird Electronics, Inc., Bellevue, Wash.) and was then followed by two oblique hauls of a 2-m ring net. This gear is equipped with a 14 m long black netting of 1.5 mm mesh size and is towed in a two-legged bridle. The ring net was hauled at a speed of 3 knots, and a flowmeter in the centre of the ring recorded the amount of water entering the net. There were no on-line measurements of depth of gear, but each haul profile was measured by a CTD mounted on the upper part of the ring. The first haul at station passed to more than 80 m deep in waters deeper than 120 m and to about 20 m above bottom in shallower areas, whereas the second haul was double-oblique, always to 35 m deep.

Based on a preliminary inspection of samples for contents of fish larvae, the site of peak abundance of sand lance (*Ammodytes* sp.) and wolffish (*Anarhichas* spp.) was identified, and after completion of the transect sampling, the vessel returned to this site with the aim of collecting larger numbers of juvenile wolffish (station marked with cross in Fig. 1). This sampling was carried out using a small midwater trawl with an opening of 10 m^2 and mesh sizes decreasing from 25 mm at the opening to 5 mm at the terminal part of the net. The gear was towed 30 min above the same position keeping the upper part of the net at depths of 10–20 m. After nine hauls with the trawl, this sampling was finished by a haul with the ring net using the same procedure. The final procedures at the station included a CTD profile and a vertically stratified sampling of mesozooplankton with a submersible pump. The pump was equipped with a net of 0.03 mm mesh size and pumped 1.2 $m^3 \cdot min^{-1}$ into the net. Sampling took place for about 3 min in each of the intervals 0–13, 13–25, 25–40, and 40–100 m.

Mesozooplankton from the pump samples was preserved in 4% formaldehyde, and in the laboratory, subsamples were identified to species and the cephalothorax length of copepods was measured to within 0.02 mm. Fish larvae and juveniles in the net samples were immediately sorted on board and preserved in 96% ethanol; the remaining plankton was preserved in 4% formaldehyde and later checked for missed larvae. The amphipods of the ring-net sample taken at peak abundance of sand lances were sorted and their total length was measured to within 1 mm. Fish larvae/juveniles from all samples were identified to species and their standard length was measured to within 1 mm. All wolffish juveniles captured during the intensive sampling program were dissected for stomach contents. The stomachs were opened with fine needles under a stereomicroscope, and the contents were identified to the nearest taxonomic level and length was measured (copepods, cephalothorax length; fish larvae, standard length; other, total length). The biomass of dominant prey items was calculated from length – dry weight regressions for *Calanus finmarchicus* (Ingvarsdottir 1998), *Parathemisto gaudichaudi* (Williams and Robins 1979), and *Ammodytes* sp. (Munk and Nielsen 1994).

For each oblique ring-net haul the abundance of fish larvae–juveniles per unit area (LPA) was calculated from number of larvae caught (LNO), length of tow measured by the flowmeter (DI), area of gear opening (AO), and maximal depth of gear during tow (MD) as

$$LPA = (LNO/(DI \cdot AO))MD$$

Calculation of prey-size preference was carried out using Chesson's index of preference, α (Chesson 1978):

$$\alpha_j = (d_j/p_j)/(\Sigma d_i/p_i) \text{ for } i = 1,\ldots,n$$

where d_j denotes the number of prey of size j in the stomach and p_j denotes the number of prey of size j in the environment.

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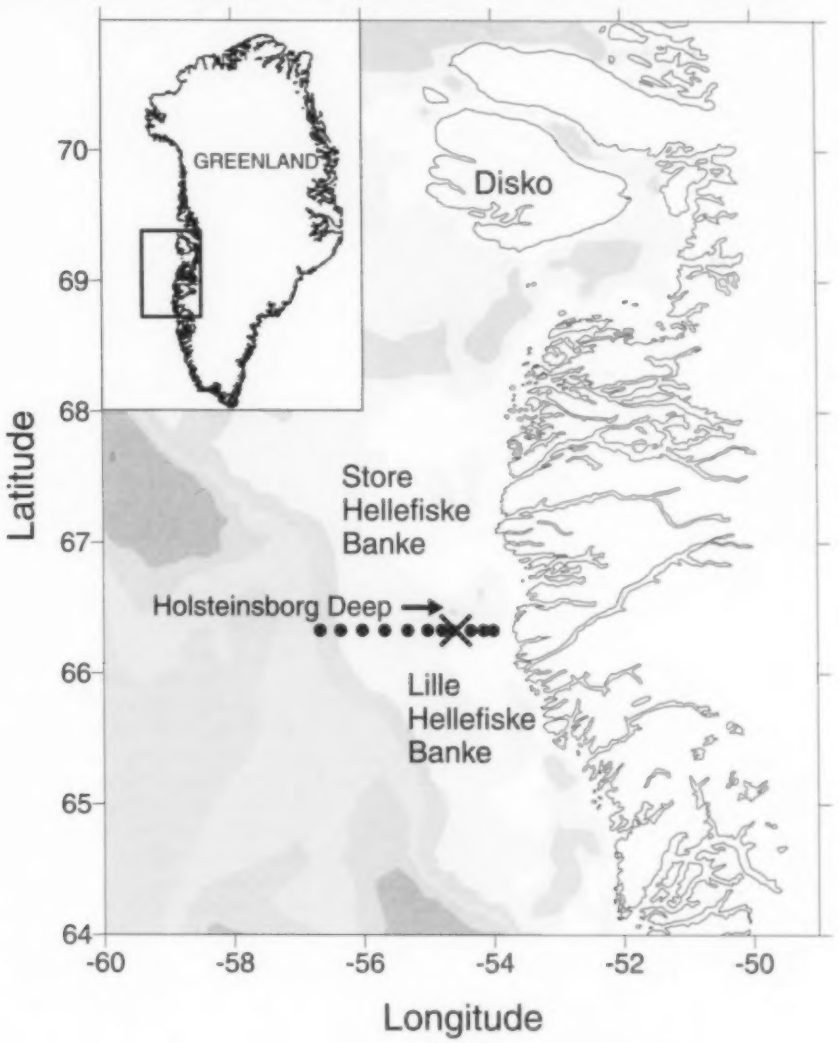
Fig. 1. The area of investigation off western Greenland. Shading indicates bathymetry, intensity changing at 100, 300, 600, 800, and 1000 m deep. Dots demarcate transect sampling positions; cross indicates the position of intensive sampling.



Results

The sampling transect crossed a part of the shelf that has a complex bathymetry (Fig. 2*a*). Our sampling started at a deep station offshelf, followed by stations at the steep shelf slope. Further inshore, the sea bottom declined again, and between 56 and 54°40′W, we passed the Holsteinsborg Deep (maximal depth 350 m). Hereafter the shelf rose steeply again to 40–50 m at the inshoremost stations. This bathymetry influenced the hydrography as illustrated by the profile of water density (Fig. 2*a*). A sharp pycnocline was evident at 20 m on the eastern part of the transect, whereas isopycnals declined in the vicinity of steep bottom slopes, i.e., at the first part of the shelf slope (~56°40′W) and at the slopes towards the Holsteinsborg Deep (~55°50′W and ~54°40′W).

The abundance estimates (per unit area) of sand lance (*Ammodytes* sp.) and wolffish (*Anarhichas* spp.) based on the second ring-net haul to 35 m were not systematically lower than corresponding estimates based on the deeper hauls. This indicates that most of these larvae/juveniles were distributed above 35 m during daytime and were well sampled by the shallow haul. Consequently, the abundance at station was determined as the average of both estimates. Along the transect we observed elevated abundances of both sand lance and wolffish above the Holsteinsborg Deep, with maximal values in the vicinity of those of the bottom slope (Fig. 2*b*). Other species of larval/juvenile fish caught along the transect included American plaice, snailfish (*Liparis* sp.), shorthorn sculpin (*Myoxocephalus scorpius*), Greenland halibut, and Arctic shanny (*Stichaeus punctatus punctatus*); these findings will not be dealt with in the present study.

Two species of wolffish were identified, Atlantic wolffish and spotted wolffish, differing by about 10 mm in mean length (Fig. 3). A total of 76 Atlantic wolffish and 18 spotted

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Fig. 2. (*a*) Vertical profiling of water density and topography along sampling transect. Isopycnals indicate density (+1000 kg·m^{-3}), solid area shows bottom depth (in metres) below surface. (*b*) Stacked bars illustrate densities of sand lance (*Ammodytes* sp.) larvae (shaded bars, in number·m^{-2}) and wolffish (*Anarhichas* spp.) juveniles (solid bars, in number·10 m^{-2}).

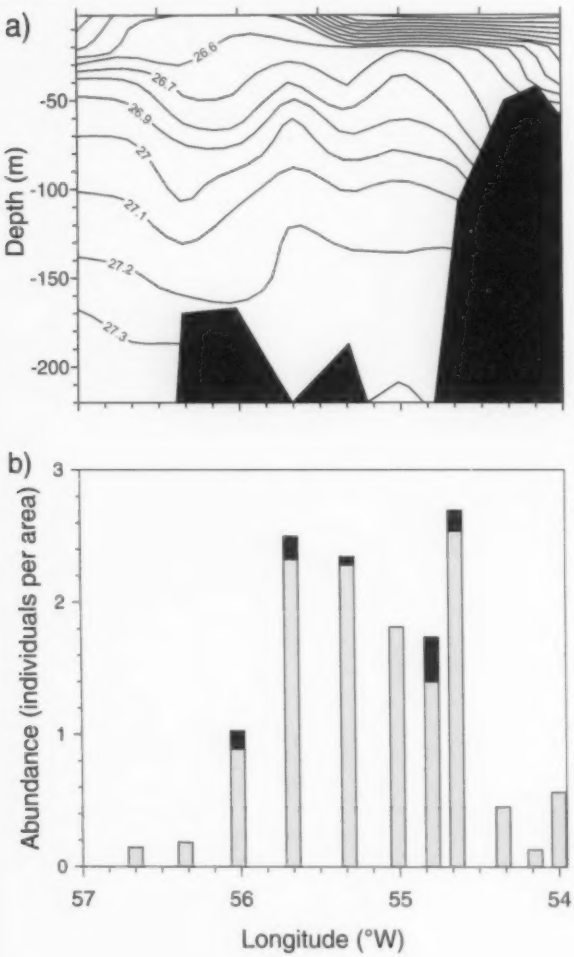
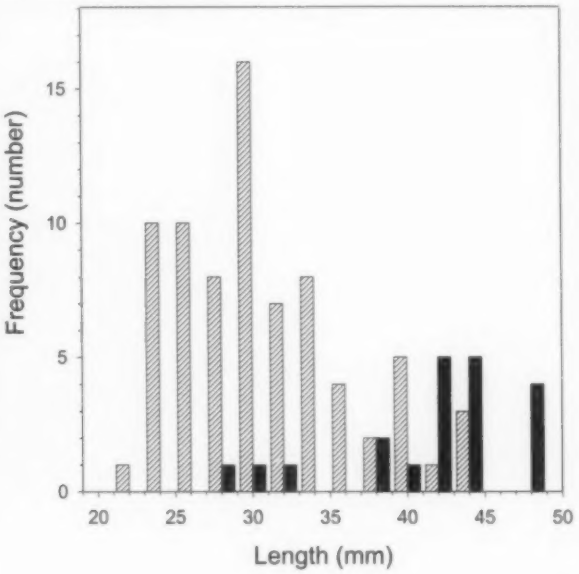


Fig. 3. *Anarhichas* spp. Size distribution of the two species of wolffish. Hatched bars illustrate frequencies of *A. lupus* (mean standard length = 31.2 mm); solid bars illustrate frequencies of *A. minor* (mean standard length = 41.6 mm).



wolffish were collected at the single selected station; the stomachs of these were dissected and the contents were analyzed. Dominant prey items (85% by number, >95% by biomass) were copepods (*Calanus* spp.), amphipods (predominantly Hyperiidae: *Parathemisto abbyssorum*), and sand lance larvae (*Ammodytes* sp.). The fish larvae registered were all identifiable to species and measurable; only six larval fragments were unidentifiable and were not included in the analyses. Other, infrequently observed prey items were gastropods, polychaetes, decapods (*Pandalus* spp.), and ostracods. Only the three dominant prey types are subjects of further analysis.

Because of the larger number of specimens and the wider size range of Atlantic wolffish, ontogenetic changes in predatory behaviour are more clearly observable for this species. Across the size range the relative contribution of the three dominant prey types changed markedly (Fig. 4; Table 1). For the smallest wolffish (below 30 mm), copepods were clearly the dominant prey. As predator size increased, so did the relative importance of amphipods and sand lance larvae. At the largest predator sizes, the amphipods dominated by number, and differences between the two wolffish species became apparent. Although Atlantic wolffish included sand lance in their diet from an early stage, only a few of the largest spotted wolffish caught sand lance larvae. On the other hand, the spotted wolffish took relatively more copepods and amphipods at larger sizes.

Viewed in a biomass perspective, the changes and differences in feeding are even more apparent. The biomass of stomach contents for the group of spotted wolffish and for two size groups of Atlantic wolffish were found by converting prey lengths to (undigested) weights (Table 1). From the table, the profitability of including fish larvae in the diet is evident. Even to the group of small Atlantic wolffish, the fish larvae were of great value in biomass and the sand lance larvae composed as much as 77% of dietary biomass in the largest wolffish. Spotted wolffish were not able to fully compensate for the lesser intake of fish larvae, even with an increased intake of copepods and amphipods the accumulated dietary biomass did not reach the same level as observed for Atlantic wolffish.

Prey sizes varied considerably, between both predator species and sizes (Figs. 5*a*–5*c*). In spite of relatively large abundances of smaller copepods (Fig. 5*d*), the wolffish only predated the largest specimens (size range 2.5–4 mm; Fig. 5*a*). We have not identified the *Calanus* species in the diet, but from the identification of species in environmental

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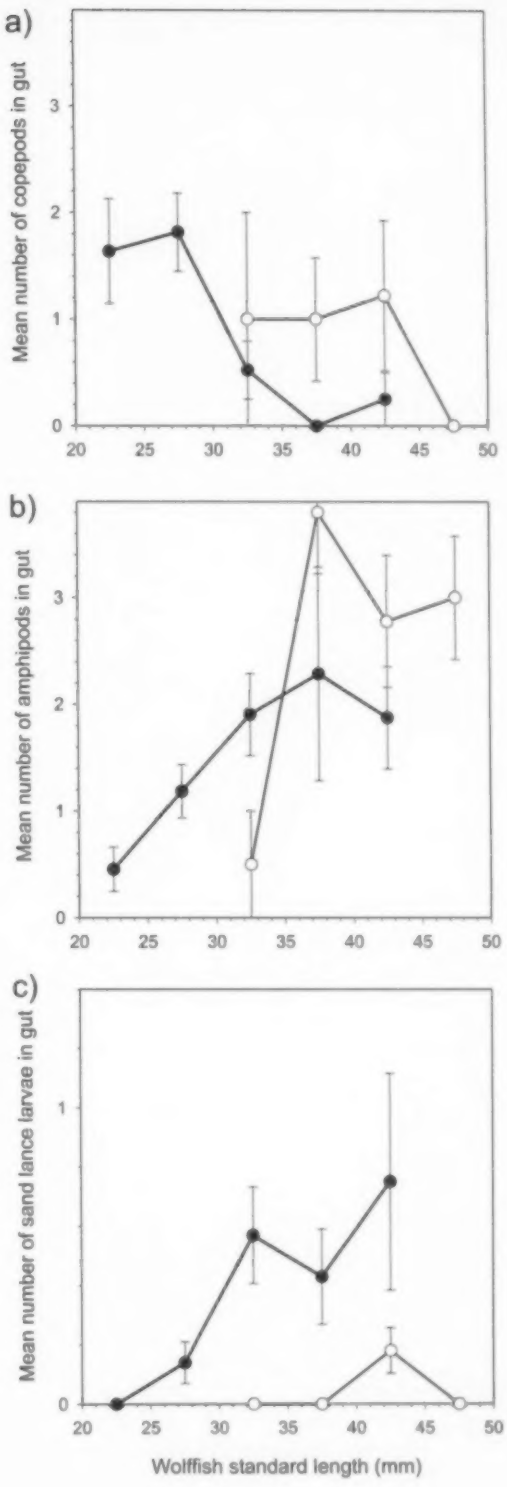

Fig. 4. *Anarhichas* spp. Abundances of dominant prey taxa in the stomachs of wolffish as a function of wolffish size: (*a*) copepods, (*b*) amphipods, and (*c*) sand lance larvae. *Anarhichas lupus* is indicated by heavy line and solid symbols; *A. minor* is indicated by thinner line and open symbols. Error bars indicate ±1 SE.

samples, it is likely that most of the diet consists of *Calanus glacialis*. This species is abundant in the size range of 2.4 to 3.6 mm (stages C3 to C5), whereas only a few *C. finmarchicus* (C5 to C6, size range 2.5–2.8 mm) are within the diet size range. The copepods above 3.6 mm (in diet and environment) are *Calanus hyperboreus* (C4–C5). Comparison between abundance estimates of copepods from the four depth strata shows that the abundance of especially larger copepods increased with depth, with maximal abundance in the 25- to 40-m stratum. Both species of wolffish fed on copepods in the same size range, with a slight, but significant ($p < 0.01$, $n = 67$), tendency of larger copepods in the diet of the larger spotted wolffish. When inspecting the copepod diet of juvenile wolffish on a relative scale, other additional patterns appear (Figs. 6*a*, 6*b*). Both length- and weight-based ratios between prey and predator decline significantly across the size range of predators ($p < 0.001$, $n = 67$). Note that the relative biomass of an ingested copepod declines up to 80% from the smallest to the largest wolffish.

For the smallest sizes of Atlantic wolffish, the amphipods in the diet were of the same size range as the copepods, but at increasing sizes, both wolffish species included larger and larger amphipods in their diet (Fig. 5*b*). This took place in spite of a declining abundance of amphipods with size (as observable for amphipods above 4 mm; Fig. 5*e*). Both the mean and range of relative amphipod sizes appear constant across the predator size range (Figs. 6*a*, 6*b*). Slopes of lines are not significantly different from zero in both the length- and the weight-based regression (for both: $p > 0.17$, $n = 75$). The average ratio of amphipod–wolffish length is 14%, and the average weight ratio is 1%.

Sand lance of the smallest sizes were included in the wolffish diet irrespective of their relative scarcity compared with other size groups (Figs. 5*c*, 5*f*). As for amphipods, wolffish consumed sand lance of larger and larger sizes during ontogeny, and findings indicate a constant ratio between prey and predator lengths (slope of regression is not significantly different from zero, $p > 33$, $n = 21$; Fig. 6*a*). The ratio of prey–predator lengths is in the order of 55%. It appears, however, that even when feeding on sand lance of increasing sizes during ontogeny, the wolffish cannot keep a constant relative biomass of the consumed prey (Fig. 6*b*). The relative biomass of the sand lance diet declined by about 50% from the smaller to the larger wolffish.

Chesson's index of preference is calculated for two size groups of Atlantic wolffish (25–35 mm and 35–45 mm), assembling information on stomach contents and environmental sand lance lengths to within 3 mm (Fig. 7). The preference spectra are skewed towards smaller sand lance sizes for both size groups of juvenile wolffish and are interpreted as the upper tails of spectra that peak at prey sizes not available in the present case. The upper limit of the spectrum of larger wolffish extends to larger prey sizes than is the case for

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Table 1. *Anarhichas* spp. Stomach contents of dominant prey items, with percent of diet included in parentheses.

	A. lupus		*A. minor*	Both species
	<35 mm long	>35 mm long	All sizes	All sizes
Abundance, no./juvenile fish				
Copepods	1.00 (46.41)	0.13 (4.45)	0.88 (22.58)	1.04 (34.40)
Amphipods	1.33 (45.86)	1.93 (68.85)	2.88 (74.19)	1.68 (55.60)
Fish larvae	0.22 (7.73)	0.75 (26.70)	0.13 (3.23)	0.30 (10.00)
Biomass, mg/juvenile fish				
Copepods	0.49 (33.47)	0.05 (1.04)	0.40 (10.77)	0.40 (16.00)
Amphipods	0.36 (24.46)	1.17 (22.40)	2.75 (73.45)	0.90 (36.00)
Fish larvae	0.62 (42.07)	4.01 (76.55)	0.59 (15.78)	1.20 (48.00)

smaller wolffish, illustrating the ability of larger wolffish to include larger and more abundant larval size groups in their diet.

Data on (*i*) the amount of sand lance in stomachs of wolffish at the specific station, (*ii*) the relative abundances of sand lance and wolffish along the transect, and (*iii*) the preference range of wolffish are used to evaluate the predation pressure on sand lance in the area of investigation. Firstly, the predation rate of a single wolffish is estimated using the mean stomach content data. Digestion rate estimates are taken from the study by Folkvord (1993), who found that 50% of 18 mm long cod larvae could be recognized in juvenile stomachs after about 2.5 h, and predation rates are calculated using the following considerations:

$$D = -\ln (0.5)/2.5 = 0.28 \text{ h}^{-1}$$

where D is the digestion rate to disappearance.

In a simple model, the predation rate (P) can be determined from mean stomach content (MSC) of both wolffish species and digestion rate (D) as

$$P = \text{MSC} \cdot D$$

If we use the MSC of both wolffish species (Table 1) and assume only minor changes in feeding rate during the 24-h period of sunlight at this latitude in July (sensu Helle 2000), this indicates a daily pressure of

$$P = 0.30 \text{ larvae} \cdot \text{wolffish}^{-1} \cdot 0.28 \text{ h}^{-1} \cdot 24 \text{ h}$$
$$= 2 \text{ larvae} \cdot \text{wolffish}^{-1} \cdot \text{day}^{-1}$$

At two sites of high predator abundance (Fig. 2*b*), the predation pressure is then estimated at 3 and 5% per day (of the total population) for the offshore and inshore group, respectively, whereas it is about 1% per day at neighbouring stations and zero when no predators are present. The preference spectra of the investigated wolffish population show, however, that the pressure is unevenly distributed across the size range of sand lances (Fig. 7). Larvae longer than ~26 mm are not targeted, and consequently the pressure is solely on the 50% of the population that is shorter than ~26 mm. The predation mortality on this group would then be in the order of 10% per day in areas of highest pressure. Even larger pressures are estimated when considering narrower size ranges of the highly preferred small-sized sand lance larvae.

Discussion

The present investigation demonstrates that juvenile wolffish are piscivores with a substantial predatory influence on the surrounding larval fish populations. The piscivory in the present case was only observed for wolffish juveniles above a certain length (20 mm); however, other observations made in areas where sand lance of smaller sizes (<10 mm long) were abundant show that wolffish less than 20 mm long also predate sand lance larvae when suitable sizes are available (P. Munk, unpublished data). Accordingly, it is not likely that ring-net sampling underestimates the abundances of smaller sand lance in the present area, the sampling of sand lances by ring net in neighbouring areas showed good catchability of smaller sand lance 8–14 mm long (P. Munk, unpublished data). During the present study, feeding of the smaller wolffish was restricted to the alternative prey, predominantly *Calanus* sp. and *Parathemisto* sp., whereas during ontogeny, the crustacean diet was gradually changed to a diet dominated by larval fish. For the larger sizes of Atlantic wolffish, fish larvae constituted about 75% of diet biomass, a level comparable to that described for specific size groups of piscivore scrombrid larvae, e.g., 91% for tuna larvae (Tanabe 2001) and 72% for Atlantic mackerel (Conway et al. 1999). On the other hand, the other wolffish species, the spotted wolffish, only infrequently predated the sand lance, and larvae did not exceed 16% of diet biomass. This difference between wolffish species, where spotted wolffish shifts to piscivory at a later stage than Atlantic wolffish, was also seen in an analysis of samples from the historical survey series of western Greenland by A. Guzman (Universidad de Los Lagos, Chile, personal communication).

The ontogenetic changes in diet composition were apparently driven by increasing preference for larger prey during growth. Small wolffish already ingested the largest copepods available, and this prey item apparently could not satisfy the demands when wolffish increased in size. Consequently, during growth the Atlantic wolffish completely abandoned copepods and instead included increasing sizes of both amphipods and fish larvae in their diet. The larger spotted wolffish, on the other hand, still ingested copepods irrespective of its declining relative biomass value, possibly because of less ability to shift to alternative (larger) prey items. A comparable, gradual change from crustacean to fish larval diet is observed for the larval stages of tuna (Young and Davis 1990) and mackerel (Fortier and Villeneueve 1996). In the field study by Young and Davis (1990), tuna larvae (~9 mm

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Fig. 5. *Anarhichas* spp. Lengths (mm) of dominant prey taxa in stomachs as function of wolffish size (in mm): (*a*) copepods, (*b*) amphipods, and (*c*) sand lance larvae. Length–frequency distributions (in mm intervals) of dominant taxa in the environment: (*d*) copepods, (*e*) amphipods, and (*f*) sand lance larvae. *Anarhichas lupus* is indicated by solid circles; *A. minor* is indicated by open rectangles. The size distribution of copepods is based on the pump sample in the 13- to 25-m depth interval. The size distributions of sand lances and amphipods are based on the last ring-net haul at station. Because of the mesh size of the net, the lower part of the amphipod size distribution is not efficiently sampled and is not shown (NA).

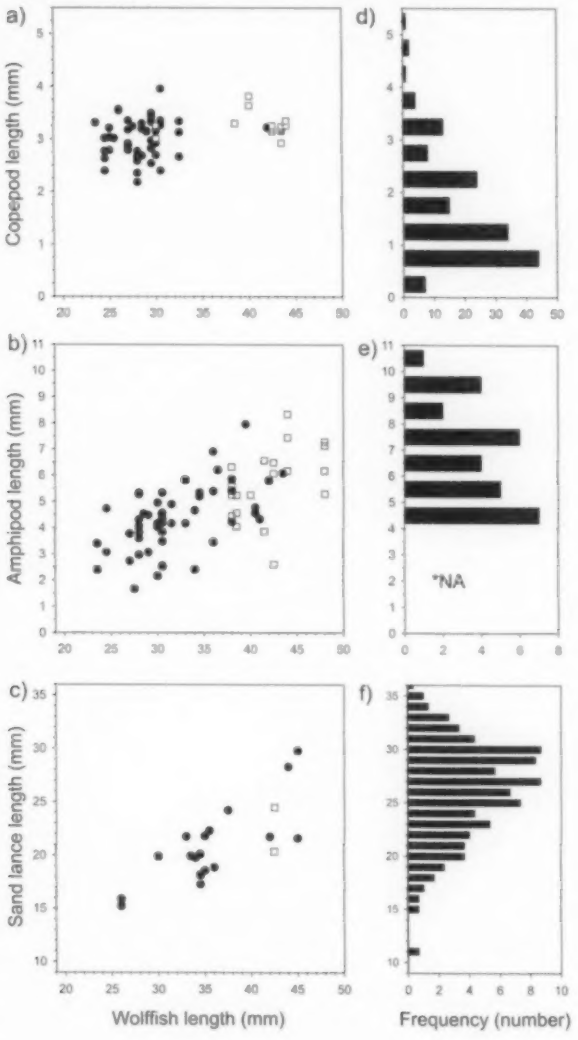
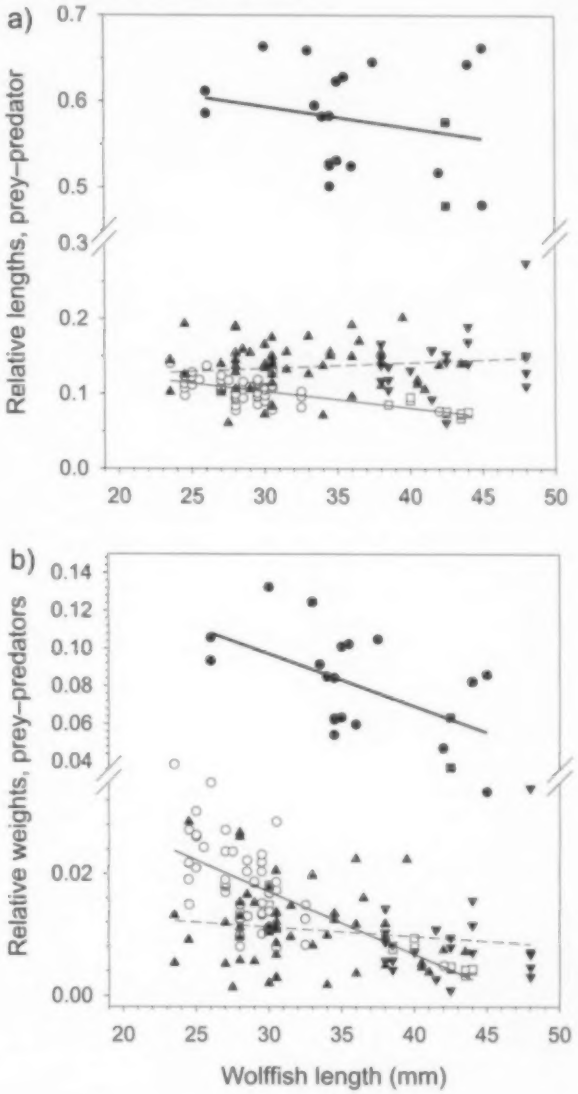


Fig. 6. *Anarhichas* spp. (*a*) Relationships between prey and predator lengths as function of wolffish length (mm). Relationships to copepods: open circles (*A. lupus*) or open squares (*A. minor*). Relationships to amphipods: triangles up (*A. lupus*) or triangles down (*A. minor*). Relationships to sand lance larvae: solid circles (*A. lupus*) or solid squares (*A. minor*). Inserted regressions are based on both wolffish species for each prey type; copepods are shown by a solid light line, amphipods by a broken line, and sand lance larvae by a solid heavy line. (*b*) Relationships between prey and predator weights as function of wolffish length (mm), symbols and lines as for (*a*).



long) predated larvae about half their own length, a prey–predator relationship that resembles the present observations on sand lance versus wolffish. These size relationships are, however, much larger than those observed during experimental studies, where a wider range of prey sizes are presented. Paradis et al. (1996) reviewed a series of laboratory–enclosure studies on predatory fish and found that fish larval vulnerability to the predator was largest at size ratios in the order of 0.1, with an ultimate largest ratio of about 0.4. As indicated by the skewness of the wolffish preference spectra, discrepancies between laboratory–mesocosm and field-based

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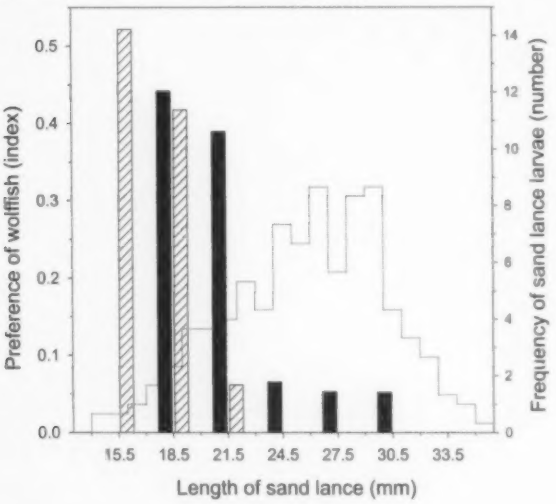
Fig. 7. *Anarhichas lupus*. Estimated index of prey size preference (Chesson's index, α) for two size groups of Atlantic wolffish, hatched bars illustrate preference of the 35 mm long size group, solid bars, the preference of the size group >35 mm. Preferences for sand lance prey are estimated in 3-mm intervals of size, bars are positioned around midpoints of intervals. Bars drawn by a dotted line illustrate the length distribution of sand lance in the ring-net sample from the same position.



findings of prey–predator size ratios might in some cases be due to unavailability of smaller (more preferred) prey sizes in the field.

To ascertain the possible magnitude of wolffish predation pressure on the sand lance larvae, a number of assumptions were made about the rate at which sand lance would be digested in wolffish stomachs. Consequently, the resulting figures of sand lance predation mortality, in the order of 3–5%·day^{-1}, should be taken with some caution. Refinement of the digestion rate estimate is, however, unlikely to challenge the magnitude of the estimated predation pressure. One aspect that is not considered in the estimation is the temperature variation between the experimental conditions under which the rate is measured and the present field conditions (6 and 3.8°C, respectively). However, when using the formula of digestive velocity given by Knutsen and Salvanes (1999), a temperature decline from 6 and 3.8°C is estimated to lead to less than 30% decline in digestion rates. Hence, although the temperature difference might affect estimates of predation pressure to some extent, the magnitude of estimated predation pressure is withheld. Total mortality estimates published for comparable-sized larvae from other populations are in the range ~4–14%·day^{-1} (e.g., Kiørboe et al. 1988; Houde 1997), and if total mortality of sand lance larvae in the present area of investigation is within this range, then the wolffish appear to be responsible for a significant part of the sand lance mortality in the area.

The observations of intensified predation pressure on the lower tail of the larval size distribution are important to the discussion on the size selectivity and growth dependence of fish larval mortality (Cowan et al. 1996; Houde 1997; Rice et al. 1997). Because of the marked size selection of the wolffish predation, the sand lance larvae must grow as fast as possible to get (or keep) out of reach of predators. On the other hand, the wolffish predators would gain more food by growing faster than the larval prey when a larger size would enable them to include more of the abundant (larger) prey size classes in their diet. Such interplay between respective growth of predator and prey cohorts would take place in many areas of co-occurring fish larval/juvenile populations (when predator and prey are born the same year), and obviously it will also take place within a cannibalistic cohort of larvae/juveniles. Modeling studies have incorporated the size-dependent interactions in predator–prey relationships (Rice et al. 1993; Crowder et al. 1994; Letcher et al. 1996), and the models illustrate how minor changes in relative sizes could cause manyfold changes in survival. Thus, because of their strong effect on mortality patterns, the size-based interactions have the potential to contribute significantly to the interannual recruitment variability (Rice et al. 1997).

Because of the variation in wolffish abundance, their predatory impact varies spatially, peaking across specific zones. Enhanced abundances of fish larvae and the predatory juveniles coincided with areas with hydrographic frontal characteristics, which are found in the vicinity of the shelf slope on both sides of the Holsteinsborg Deep. Such linkages between hydrographical and biological characteristics have been observed during other investigations off western Greenland, where species composition of fish larvae showed a marked cross-shelf structuring, and their abundances peaked in the vicinity of hydrographic fronts (P. Munk, B.W. Hansen, T.G. Nielsen, and H.A. Thomsen, unpublished data). The frontal zones are areas of enhanced productivity with rich food supply for the fish larvae, and consequently these offer the larvae improved growth conditions (Fortier et al. 1992; Munk and Nielsen 1994; Okazaki et al. 1998). Although frontal zones might be optimal habitats for larval feeding and growth, the present study shows how potential predators of the larvae are also likely to accumulate in this zone, where feeding conditions are beneficial to them. Thus, the larvae residing in frontal zones face positive consequences with respect to feeding and growth and negative consequences with respect to direct predation mortality, the balance between these determining long-term survival of the population.

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Hierarchical Bayesian analysis of capture–mark–recapture data

E. Rivot and E. Prévost

Abstract: We present a hierarchical Bayesian model (HBM) for capture–mark–recapture (CMR) data analysis. It aims at estimating the probability of capture (θ_i) and the total population size (N_i) in a series of I years $i = 1,\ldots,I$. The HBM assumes that the θ_is and N_is are sampled from a common probability distribution with unknown parameters. It is compared with the model assuming independence between years in the θ_is and N_is (ABM). We show how a transfer of information between years is organized by the HBM. We compare the merits of HBM vs. ABM to estimate the spawning run and smolt run of an Atlantic salmon (*Salmo salar*) population of the River Oir (France) over a period of 17 years. In the spawners case, yearly data are poorly informative. Consequently, the HBM greatly improves posterior inferences compared with the ABM in terms of dispersion and robustness to the choice of prior. In the smolts case, the HBM does not significantly improve inferences compared with the ABM because data are more informative. We discuss why hierarchical modeling should be recommended in any ecological study where the data are collected on several sampling units that share some common features.

Résumé : Nous proposons un modèle Bayesien hiérarchique (HBM) pour analyser des données de capture–marquage–recapture. Ce modèle permet d'estimer la probabilité de capture (θ_i) et la taille de la population (N_i) pour une série de I années $i = 1,\ldots,I$. Le HBM suppose que les θ_is et les N_is sont issus a priori d'une même distribution de probabilité dont les paramètres sont inconnus. On le compare à un modèle qui suppose l'indépendance des θ_is et des N_is a priori (ABM). Nous montrons comment le HBM organise le transfert d'information entre les années. Nous comparons les avantages respectifs du HBM et du ABM pour estimer les migrations d'adultes et de smolts de la population de Saumon atlantique (*Salmo salar*) de la rivière Oir (France). Dans le cas des adultes, les données annuelles sont peu informatives. Le HBM améliore les inférences par rapport au ABM, en terme de dispersion et de robustesse au choix des distributions a priori. Dans le cas des smolts, le HBM n'améliore pas significativement les inférences par rapport au ABM car les données annuelles sont plus informatives. Finalement, nous recommandons d'utiliser un modèle hiérarchique pour analyser des données en écologie dans tous les cas où les données traitées concernent des unités qui partagent une caractéristique commune.

Introduction

The Bayesian approach has a great potential for the treatment of capture–mark–recapture (CMR) models. Although it is one of the main features of Bayesian data analysis, hierarchical modeling seems to have aroused little interest for CMR data. This paper investigates the potential of Bayesian hierarchical modeling applied to estimating the size of a population in a series of years, either consecutive or not, for which yearly CMR data have been collected under the same experimental design.

The Bayesian framework may significantly improve statistical inferences from CMR data analysis (Smith 1991; Pollock 1991; Garthwaite et al. 1995). Bayesian estimators perform better than classical ones in data-poor situations (Gazey and Staley 1986; Chao 1989). Indeed, classical point estimators are mostly based on asymptotic approximations. Therefore, bias can be relatively large when sample sizes are small (Seber 1982). Confidence intervals around maximum likelihood estimates can also be inaccurate when they do not account for the skewness of the underlying likelihood distribution (Sprott 1981; Smith 1988). In contrast, Bayesian posterior inferences about the quantities of interest naturally reflect the entire shape of their distributions. The development of intensive computation methods now offers numerical procedures for solving a wide variety of inference problems within the Bayesian framework. Importance sampling or Markov chain Monte Carlo (MCMC) methods (Gelman et al. 1995) enable easy sampling from posterior distributions even in the most complex multiple CMR census models (George and Robert 1992; Basu and Ebrahimi 2001). By comparison, standard analytical approaches, such as maximum likelihood techniques, may become rapidly untractable when model complexity increases.

Relatively long but sparse (small sample size) series of data are quite common when dealing with CMR surveys

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aimed at estimating wild populations over a series of years. To analyze such data sets, one may first be tempted by considering the complete independence between years, i.e., a model where the CMR experiment performed each year is totally unrelated to those of the other years. At another extreme, one can ignore the between-year variability by pooling all years. An exchangeable hierarchical model is a sensible compromise between these radically contrasted views (Gelman et al. 1995). It assumes that the years are neither completely identical nor fully unrelated, but considers the yearly unknown variables as a random sample from a common probability distribution. In data-poor situations, the model assuming independence between years may lead to poor posterior inferences. Indeed, little information may be brought by the data in certain years, what may in turn result in highly imprecise or unreliable posterior distributions. Another serious drawback is that results may be highly sensitive to the prior choice (Gazey and Staley 1986; Chao 1989) and thus widely open to criticism because there is not a unique accepted way for assigning prior probabilities.

In this paper, we show two ways in which hierarchical modeling can significantly improve the inferences. First, the hierarchical approach can transfer valuable information from neighboring data to estimate the total population size in years for which CMR data are poor. Second, it offers a sensible solution to the critical problem of the sensitivity of the posterior inferences to the prior choice. Smith (1991) and George and Robert (1992) presented a hierarchical model for the catchability in the context of a multiple mark–recapture census of a closed population. However, the authors do not really discuss how hierarchical structure may improve the analysis of CMR data. Although he explicitly did not set his study in a CMR framework, Raftery (1988) already proposed a hierarchical model for N when it is estimated from a multiple Binomial sampling with a constant probability of "success". He pointed out that the hierarchical structure is an interesting alternative to classical choices of discrete bounded prior on N. Indeed, it allows a convenient representation of a vague prior on N, avoiding the critical problem of the high sensitivity of inferences to the choice of the bounds. More recently, Su et al. (2001) applied hierarchical modeling to account for similarities in run timing among years for pink salmon (*Oncorhynchus gorbuscha*) escapement. The authors illustrated well how the hierarchical method significantly enhances the ability to estimate escapement for years where only few data are available.

We set a model that can accommodate any case where the CMR experiments are performed over a series of years following a homogeneous design similar to the two-sample Schnabel census for a closed population, i.e., the simple Petersen experiment (Seber 1982). We first concentrate on the conceptual framework of the hierarchical modeling without entering into technical details. The hierarchical model, jointly treating all years, appears as the most general model. We highlight that the model treating all years independently can be considered a particular case of the hierarchical model. We show how the between-year dependency introduced by the hierarchical assumption organizes a transfer of information between years. It enables one to make use of the full historical information to construct a modified prior distribution that should improve yearly inferences.

We apply our methodology to two contrasted numerical case studies. We treat two data sets of CMR surveys designed to estimate the spawning run and the smolt run of an Atlantic salmon (*Salmo salar*) population of the River Oir (France) over a period of 17 years. We focus on the comparison between the posterior inferences obtained under the hierarchical model and the model assuming between-year independence. Posterior inferences are carried out by Markov chain Monte Carlo (MCMC) methods (Gelman et al. 1995). As the problem of setting the priors is always crucial in Bayesian analysis, we carefully investigated the sensitivity of our results to the prior choices in an expanded appendix.

Materials and methods

CMR framework

We consider a data set from a population survey to estimate the size of the same population in a series of I years (typically I would be between 10 and 100). In the following, the subscript i stands for the year i. The data available come from CMR experiments analogous to the well-known two-stage Petersen experiment. A first-capture sample is carried out by means of a trap. Some of the individuals caught are marked and released. Recaptures of marked individuals are then carried out. Hypotheses needed to assume a Petersen-type model for a given year are supposed to be verified (they will be detailed later in the numerical examples). The unknown size of the population in year i is denoted N_i, and the CMR data collected for the same year are denoted d_i. We characterize the trap by a trapping efficiency, denoted θ_i, that can be interpreted as the probability of each individual to be caught. The entire series of unknown variables of interest are denoted $\theta = \{\theta_i\}_{i=1,\ldots,I}$ and $N = \{N_i\}_{i=1,\ldots,I}$ and data are denoted $\{d_i\}_{i=1,\ldots,I}$.

The CMR data are used to make inferences on both the trap efficiencies θ and the population sizes N. In the following, we first develop an exchangeable hierarchical Bayesian model (HBM) that combines all years to derive joint inferences about the entire series (N,θ). By jointly treating all of the years, the HBM provides a mean to estimate each (N_i,θ_i) by taking advantage of the information coming from the data of the other $I - 1$ years (denoted $\{1,\ldots,I\}_{\neq i}$ in the following). Then, we derive a second model that can be considered a particular case of the HBM, referred as the annual Bayesian model (ABM). The ABM is less parsimonious than the HBM. It assumes that the θ_is and N_is are independent between years: posterior inferences about variables are derived independently for each year i using only the data from the year in turn. A completely pooled Bayesian model, ignoring the between-year variability, can also be considered an extreme particular case of an exchangeable model. It is the most parsimonious model but is of little interest and is therefore not further investigated.

The following notations hold in the sequel. $P(\cdot|\cdot)$ denotes a conditional probability distribution and $\pi(\cdot)$ a prior distribution, with arguments determined by the context. Let us denote as X any random variable that we seek to estimate and as y the observations available to estimate X. The unnormalized Bayesian posterior density of $X|y$ is

$$P(X|y) \propto \pi(X)P(y|X) \quad (1)$$

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Table 1. Hierarchical Bayesian model.

Notations

$N = \{N_i\}_{i=1,\ldots,I}$, $\theta = \{\theta_i\}_{i=1,\ldots,I}$, data $= \{d_i\}_{i=1,\ldots,I}$

Hyperparameters $\phi = (\delta,\gamma)$

Joint prior distribution for (N,θ,ϕ)

Independence assumption

(T1.1) $\pi(N,\theta,\phi) = \pi(N,\delta)\pi(\theta,\gamma)$

Exchangeability assumption

(T1.2) $\pi(N,\theta,\phi) = \pi(\delta)\prod_{i=1}^{I}\pi(N_i|\delta)\pi(\gamma)\prod_{i=1}^{I}\pi(\theta_i|\gamma)$

Likelihood

(T1.3) $L(N,\theta,\phi|\text{data}) = L(N,\theta|\text{data}) = \prod_{i=1}^{I}L(N_i,\theta_i|d_i) = \prod_{i=1}^{I}L_i$

Posterior distribution

(T1.4) $P(N,\theta,\phi|\text{data}) \propto \pi(\gamma)\pi(\delta)\prod_{i=1}^{I}\pi(N_i|\delta)(\theta_i|\gamma)L_i$

(T1.5) $P(N,\theta|\text{data}) \propto \int[\pi(N,\theta,\phi)L(N,\theta,\phi|\text{data})]d\phi$

Note: The notation $d\phi$ means that the integration is made with respect to the variable ϕ.

The symbol $\propto$ means that both terms are proportional. The coefficient of proportionality is a normalizing factor ensuring that the posterior $P(X|y)$ integrates to one. It depends on y only and is thus a constant with regard to X. $P(X|y)$ is the sampling distribution, i.e., the joint distribution of the observations y conditionally on X. When regarded as a function of X, $P(X|y)$ is called the likelihood and is denoted $L(X|y)$.

Exchangeable HBM

The HBM assumes a hierarchical structure on both the trapping efficiencies and the total population sizes. This model combines all years together through a methodology of estimation that explicitly accounts for the similarities in the CMR experiments and for the dependence among the population sizes.

Basically, the hierarchical assumption is a conditional structure on the probability distribution (Gelman et al. 1995). Let us first consider the hierarchical hypothesis on the trapping efficiencies. The HBM assumes that the θ_is are sampled from a common population distribution $\pi(\theta_i|\gamma)$, conditional on unknown hyperparameters γ. In turn, a prior $\pi(\gamma)$ is assigned to the hyperparameters. The θ_is arise from analog experiments using the same trapping gear and the same experimental protocol. The hierarchical structure of the probability distribution sets the dependency between the θ_is by expressing both similarity and heterogeneity among the θ_is. It allows for between-year variations of the θ_is resulting from unpredictable changes in environmental conditions or fish behavior (e.g., river discharge or temperature). The HBM considers γ as random with a prior that will be updated by the data of all years. This updating of the hyperparameters distribution (details follow) allows transferring of information between years.

A hierarchical structure is also imposed on the total population size $N = \{N_i\}_{i=1,\ldots,I}$. The population investigated during the period $i = 1,\ldots,I$ is the same population but observed in different years. The size of the population is generated and constrained by some common ecological processes whatever the year. Thus, the estimation that one may derive for the years $\{1,\ldots,I\}_{\neq i}$ are also partially informative with regards to the population size of a given year i. It is then appropriate to model a priori the N_is as issuing from a common population distribution $\pi(N_i|\delta)$ with unknown random hyperparameters δ with their own prior $\pi(\delta)$.

The HBM jointly treats the entire time series $i = 1,\ldots,I$. All variables (N_i,θ_i) depend on the hyperparameter vector denoted $\phi = (\gamma,\delta)$. The joint posterior $P(N,\theta,\phi|\text{data})$ in eq. 2 (detailed in Table 1) is obtained by the combination of the joint prior $\pi(N,\theta,\phi)$ and the likelihood term $L(N,\theta,\phi|\text{data})$

(2) $P(N,\theta,\phi|\text{data}) \propto \pi(N,\theta,\phi)L(N,\theta,\phi|\text{data})$

The definition of the joint prior $\pi(N,\theta,\phi)$ relies on two common hypotheses. We assume first the independence between (θ,γ) and (N,δ) in T1.1 and second the exchangeability of the θ_is and the N_is in T1.2 (Gelman et al. 1995). Let us first detail the exchangeability for the θ_is. The joint prior for (θ,γ) reflects the dependence among the θ_is. Exchangeability is a weaker concept than statistical independence. It is based on the hypothesis that before seeing the results of the CMR experiments, i.e., in the absence of data, there is no argument to distinguish a priori the θ_is. Mathematically, exchangeability means that the joint distribution of the θ_is remains unchanged by any permutation of the i indices. Unlike in a sequential Bayesian model, the order by which data have been gathered does not bear any significance. As suggested by Gelman et al. (1995), the most appropriate exchangeable distribution for (θ,γ) considers each θ_i as independently sampled from the conditional population distribution governed by γ, $\pi(\theta_i|\gamma)$. We made the same exchangeability assumption for the N_is. Combined with the independence between (θ,γ) and (N,δ), the exchangeability assumption leads to the joint prior in T1.2.

The likelihood term $L(N,\theta,\phi|\text{data})$ is the product of the yearly likelihood functions $L(N_i,\theta_i,\phi|d_i)$ denoted L_i in the following. The L_is stem from the stochastic model underlying the sampling process of the CMR experiments. Thus, the likelihood does not depend on the hyperparameter vector ϕ, and the simplification in T1.3 holds. The sampling distributions that we use in this paper are the standard Binomial and Hypergeometric distributions (see, for instance, Gazey and Staley 1986). The likelihood functions and the underlying hypotheses are detailed in the section devoted to the numerical applications.

The resulting full joint posterior distribution of (N,θ,ϕ) is detailed in T1.4. The posterior distribution of the quantities of interest in T1.5 is obtained by integrating out the full joint posterior with respect to the hyperparameter vector ϕ (considered nuisance parameters).

ABM

The ABM that assumes the between-year independence of both the θ_is and N_is can be considered a particular case of the most general exchangeable hierarchical model. The ABM assumes a priori that the θ_is and N_is are fully unrelated. Under this hypothesis, the CMR data of the year i are only relevant to estimating the corresponding θ_i and N_i. The

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Table 2. Hierarchical Bayesian model.

Predictive

Marginal predictive prior distribution for unknown observable variables $(\tilde{N},\tilde{\theta})$

(T2.1) $\pi(\tilde{N},\tilde{\theta}) = \int [\pi(N,\theta|\phi)\pi(\phi)]d\phi$

Posterior predictive distribution conditional on the observed data

(T2.2) $P(\tilde{N},\tilde{\theta}|\text{data}) = \int [\pi(N,\theta|\phi)P(\phi|\text{data})]d\phi$

Marginal posterior distribution of year i

For each i in 1,...,I, the marginal of the variables of interest writes

(T2.3) $P(N_i,\theta_i|\text{data}) = \int [\int [P(N,\theta,\phi|\text{data})]\ d\{N_k,\theta_k\}_{k\neq i}]d\phi$

Extracting the term in "i" from the posterior $P(N,\theta,\phi|\text{data})$ yields

(T2.4) $P(N,\theta,\phi|\text{data}) \propto \pi(\phi)\pi(N_i,\theta_i|\phi)L_i \prod_{k\neq i} [\pi(N_k,\theta_k|\phi)L_k]$

We denote as data_i^* the data of all years except i. The term L_i in T2.4 does not depend on ϕ. By extracting it from the integral on ϕ in T2.3, it becomes

(T2.5) $P(N_i,\theta_i|\text{data}) \propto \pi^*(N_i,\theta_i,\text{data}_i^*)L_i$

where the term $\pi^*(N_i,\theta_i,\text{data}_i^*)$ equals

(T2.6) $\pi^*(N_i,\theta_i,\text{data}_i^*) = \int [\pi(N_i,\theta_i|\phi)\int [\pi(\phi)\prod_{k\neq i} (\pi(N_k,\theta_k|\phi)L_k)]\ d\{N_k,\theta_k\}_{k\neq i}]d\phi\ = \int [\pi(N_i,\theta_i|\phi)P(\phi|\text{data}_i^*)]d\phi$

Note: Predictive distribution and expression of the marginal $P(N,\theta|\text{data})$. The notations $d\phi$ and $d\{N_i,\theta_i\}_{k\neq i}$ mean that the integrations are made with respect to the variable ϕ and $\{N_i,\theta_i\}_{k\neq i}$, respectively.

ABM still needs to assign a prior to each θ_i and N_i, but it no longer assumes random hyperparameters common to all years. By analogy with the HBM setting, those annual priors are denoted $\pi(N_i|\delta_i^0)$ and $\pi(\theta_i|\gamma_i^0)$, where the parameters $\phi_i^0 = (\delta_i^0,\gamma_i^0)$ are fixed to particular values, either equal or not between years. This impedes any transfer of information between years, and inferences about a particular year i fully ignore what can be learned from experiments carried out in the years $\{1,...,I\}_{\neq i}$. When the same population is surveyed during several years, assuming the between-year independence is counterintuitive and can result in a loss of information. In contrast, by structuring the between-year dependency, the HBM acknowledges that the CMR experiments of years $\{1,...,I\}_{\neq i}$ are partially informative with regards to the trapping efficiency and the population size of year i. The pattern of dependence and the amount of information that is transferred between years will be set a posteriori through the updating procedure of the hyperparameters.

One may also build "hybrid" models that make the independence assumption for only one of the two components θ and N, the other one still being modeled under a hierarchical structure. We compare inferences obtained under the HBM, the ABM, and the two "hybrid" models to investigate which of the two components, θ or N, is the most sensitive to independence vs. hierarchical modeling.

Choice of priors and sensitivity analysis

Setting the prior distributions is a critical point of any Bayesian analysis. All priors $\pi(\theta_i)$ and $\pi(N_i)$, conditional priors $\pi(\theta_i|\gamma)$ and $\pi(N_i|\delta)$, and hyperpriors $\pi(\gamma)$ and $\pi(\delta)$ used in numerical applications are detailed in Appendix A. We investigated how the posterior inferences obtained in the ABM and HBM are sensitive to the choice of priors. This issue is also deferred to Appendix A.

Interpreting the HBM

Inferences about new observable variables denoted $(\tilde{N},\tilde{\theta})$ can be derived through the predictive distribution conditional on the observed data (Gelman et al. 1995). It is an average of the conditional population distribution $P(N,\theta|\phi)$ over the posterior distribution of the hyperparameter ϕ conditioned on all observed data. The difference between the marginal prior in T2.1 and the posterior predictive in T2.2 reflects the amount of information brought by the data of all years to update the prior distribution common to all years (Table 2).

In the HBM, the data of all years are included to estimate the variables of interest (N_i,θ_i) for any particular year i. As shown in T2.3–T2.5, the marginal posterior $P(N_i,\theta_i|\text{data})$ in the HBM can be rewritten as the product of two terms: the likelihood term L_i and a complex integral term denoted $\pi^*(N_i,\theta_i,\text{data}_i^*)$. In this integral, all random variables except (N_i,θ_i) are integrated out, and the integration depends on data of years $\{1,...,I\}_{\neq i}$, denoted data_i^*. Thus, it can be considered a function of (N_i,θ_i) and data_i^*. The term $\pi^*(N_i,\theta_i,\text{data}_i^*)$ should be interpreted as a "modified" prior on (N_i,θ_i). Equation T2.6 points out that $\pi^*(N_i,\theta_i,\text{data}_i^*)$ is the marginal prior of (N_i,θ_i) obtained by integrating over ϕ when ϕ is distributed as $P(\phi|\text{data}_i^*)$, i.e., the posterior obtained with data of each year k in $\{1,...,I\}_{\neq i}$. Note that the contribution of each of the years $\{1,...,I\}_{\neq i}$ to this modified prior is judiciously weighed according to L_k, i.e., according to how informative each year is about the population size and the trapping efficiency. It is through the modified prior $\pi^*(N_i,\theta_i,\text{data}_i^*)$ that the information from the data of years $\{1,...,I\}_{\neq i}$ is trans-

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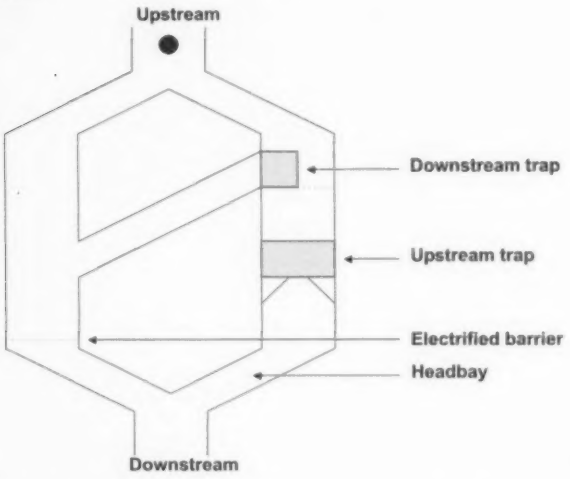
Fig. 1. Scheme of the Cerisel trapping facilities working as a double upstream and downstream partial counting fence. ● indicates the released site of tagged smolts and spawners. The released site and the downstream trap are 1 km away from each other.



ferred into the estimation of the variables (N_i,θ_i). The higher the information carried by the posterior $P(\phi|\text{data}_i^*)$, the more informative the modified prior distribution $\pi^*(N_i,\theta_i,\text{data}_i^*)$.

In the ABM, the posterior of (N_i,θ_i) is the combination of L_i with a prior $\pi(N_i,\theta_i|\phi_i^0)$ where ϕ_i^0 is fixed to a particular value. Under such a model, the analyst often faces the dilemma between choosing ϕ_i^0 so that $\pi(N_i,\theta_i|\phi_i^0)$ is uninformative and taking the risk of unreliable inferences in data-poor situations, and choosing ϕ_i^0 that brings substantial information a priori and taking the risk of influencing the inferences by personal judgment not formally related to the data in hand. The HBM proposes an intermediate approach as a sensible solution to this dilemma by assigning higher degrees of credibility to some values of hyperparameters according to the data available.

Numerical examples

An Atlantic salmon population survey

We apply the framework of the previous section to a data set coming from the survey of the Atlantic salmon population on the Oir River (Normandy, France) since 1984. The Oir River is a spawning tributary of the Sélune River, which flows into the English Channel. The characteristics of the watershed are described in Baglinière et al. (1993). Spawners enter into Oir River to spawn during late fall and early winter (October–December). Smolts migrate out to the sea in the springtime (mainly in April). Both smolt and spawner runs are composed of several age classes (see Baglinière et al. 1993 and Prévost et al. 1996), but the age structure is not considered in this study.

The Cerisel trapping facility is located 2.3 km upstream from the confluence with the Sélune River and 12.3 km downstream from an impassable dam. The trapping facility consists of a double upstream and downstream partial counting fence (Baglinière et al. 1993) (Fig. 1). The inward and outward salmon migrations to and from the entire area above the trap are monitored. The downstream trap is used to capture smolts during seaward migration but also spent adults after spawning. The upstream trap is used to capture spawners swimming upstream. Both upstream and downstream traps are operated every day during the migration time so that no pulse of migration is missed. Data currently available are from 1986 to 2001 for the smolt run and from 1984 to 2000 for the spawning run (Tables 3 and 4). They have been consistently gathered under a homogeneous experimental design through the entire study period.

Table 3. Capture–mark–recapture data for spawners by spawning migration year.

Year	c_i	x_i	m_i	r_i	rm_i
1984	167	13	154	22	12
1985	264	48	216	25	21
1986	130	37	93	9	5
1987	16	4	12	24	2
1988	226	43	183	12	12
1989	235	36	199	56	56
1990	15	8	7	17	2
1991	44	0	44	24	23
1992	31	11	20	9	4
1993	100	19	81	7	4
1994	32	14	18	5	1
1995	109	7	102	46	39
1996	70	15	55	82	25
1997	56	22	34	15	12
1998	34	4	30	36	6
1999	154	6	148	35	23
2000	53	0	53	37	4

Note: c_i denotes the number of spawners caught at the upstream trap; x_i denotes the number of spawners that died during manipulation or that are removed for experimental use or hatchery production; m_i is the number of spawners marked and released ($m_i = c_i - x_i$); r_i is the recapture sample; and rm_i the number of fish marked among r_i. See text for more details about the experiments.

The CMR experiments are different in their details for the smolts and the spawners, thus leading to distinct models. The two following sections describe the data, the stochastic models, and the subsequent sampling distributions that define the likelihood terms L_i (Table 5).

Spawning run

For each year i from 1984 to 2000, c_i denotes the number of spawners caught at the upstream trap. A number x_i of fish trapped is not released upstream either because they die during manipulation or because they are removed for experimental use or hatchery production. m_i denotes the number of fish marked and released ($m_i = c_i - x_i$). The fish released upstream from the trap are individually tagged. The recapture sample is gathered during and after spawning. Let us denote as r_i the sum of all those fish recaptured or observed (see thereafter) and as rm_i the fish marked among r_i. Our model leading to the likelihood L_i in T5.3 requires a few somewhat simplifying hypotheses (H1–H4). H1: all of the N_i spawners are assumed to be independently and equally catchable in the trap, with a probability θ_i. θ_i is considered constant over the migration season. H2: the spawner population upstream

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Table 4. Capture–mark–recapture data for smolts by migration year.

Year	c_i	m_i	rm_i
1986	887	135	91
1987	283	31	24
1988	307	59	43
1989	553	65	43
1990	746	38	35
1991	151	35	27
1992	580	50	43
1993	209	26	24
1994	329	17	10
1995	618	63	53
1996	767	76	58
1997	205	63	31
1998	511	63	31
1999	195	59	45
2000	1849	300	232
2001	688	264	123

Note: c_i denotes the number of smolts caught at the downstream trap; m_i is the number of smolts marked and released; and rm_i the number of marked recaptured. See text for more details about the experiments.

from the trap is closed to change in size. No spawner runs downstream after getting over the trap. There is neither mortality following marking nor natural mortality between the time of marking and recapture for marked or unmarked spawners. H3: there is no tag shedding. H4: the recapture (or resighting) probability is the same for all the fish whether or not marked.

Under the "equal catchability assumption" H1, one can consider the migration of the N_i spawners as independent Bernoulli experiments with probability of "success" θ_i. Accordingly, c_i is the observed result of a Binomial experiment in which each of the N_i spawners has a probability θ_i of being caught (T5.1).

Hypotheses H2–H3 enable one to consider that the number of spawners present on the spawning grounds above the trap is $N_i - x_i$ and that m_i are marked among them. In practice, the recapture sample is obtained by three methods: electrofishing on the spawning grounds, collection of dead fish after spawning, and trapping of spent fish at the downstream trap of the Cerisel facility. Each of the three recapture methods randomly samples within a fraction of the $N_i - x_i$ fish. Electrofishing samples the fish alive on the spawning grounds. Recovery of carcasses samples fish dead after spawning not previously caught alive. Downstream trapping samples the fish having survived to spawn and not previously caught alive. As a first approximation to this more complicated scheme, our modeling approach works as if the aggregated recapture sample r_i was randomly drawn from the entire population $N_i - x_i$. Under this premise and further assuming H4, one can consider the recapture sample r_i containing rm_i marked fish as a random sample from a population of total size $N_i - x_i$ in which m_i fish are marked. Because every fish recaptured is pelvic-fin clipped, recapture is a sampling without replacement. The recapture experiment is thus modeled by a Hypergeometric distribution (T5.2).

Smolt run

For each year i between 1986 and 2001, c_i denotes the number of smolts caught in the downstream trapping facility during the migration time. Among the c_i smolts captured, a number $m_i \leq c_i$ have been tagged (mostly fin-clipped) and released upstream from the trapping facility used for capture (Fig. 1). Some of them will be recaptured at the same downstream trap. Note that the recapture is not conducted at a location downstream from the trap as it is often the case in mark–recapture experiments. We denote as rm_i the number of tagged and released smolts that are recaptured ($rm_i \leq m_i$). We make four classical assumptions analogous to H1–H4. H1′: we assume equal catchability at the downstream trap (hypothesis analogous to H1). H2′: the population is closed during the migration time. There is neither mortality induced by the capture–marking procedure nor natural mortality between the time of marking and recapture for either marked or unmarked smolts. H3′: there is no tag shedding and all smolts marked and released will migrate out. H4′: all m_i marked and released smolts have the same probability of being recaptured at the downstream trap. We suppose that the capture and marking does not affect the behavior of the smolts in a way that would change their vulnerability to the trap. Thus, the probability of recapture of previously marked and released smolts is the same as the probability of capture of unmarked smolts exposed to the trap for the first time.

Under H1′, the first term of the likelihood L_i corresponds to a Binomial sampling distribution (T5.1′). Under H2′–H4′, one can model the recapture experiment as a Binomial one with m_i trials and rm_i successes. H4′ allows one to use in the recapture Binomial model (T5.2′) the same probability of "success" θ_i as in the capture Binomial model. It is a crucial hypothesis for the estimation procedure. Intuitively, T5.2′ will be used to estimate θ_i, and T5.1′ will be used to estimate N_i conditionally on θ_i.

MCMC simulations and implementation with the software WinBUGS®

Once the step of describing the stochastic model is achieved, our model is easily implemented and fitted using an MCMC algorithm. We used the WinBUGS® software (Spiegelhalter et al. 2000, available at http://www.mrc-bsu.cam.ac.uk/bugs) that samples from the joint posterior distribution using the Metropolis-within-Gibbs sampling algorithm. The WinBUGS® code for all models described in this paper is available from the authors upon request. The basic idea behind the Gibbs sampling algorithm is to generate random draws for all unknown variables by cyclically sampling from the unidimensional full posterior conditional distributions of all variables. The latter are obtained by extracting from the joint posterior distribution the term involving only the variable in turn while treating all others terms as constant. Meyer and Millar (1999) reported on significant progress made in facilitating the routine implementation of Bayesian analysis thanks to the WinBUGS® software (see also the review by Gentleman 1997). It simplifies the implementation of the Gibbs sampling by alleviating

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Table 5. Observation model and sampling equations for the capture–mark–recapture (CMR) experiments for spawners and smolts.

	Spawners		Smolts
Observations	$d_i = (c_i, x_i, m_i, r_i, rm_i)$		$d_i = (c_i, m_i, rm_i)$
Capture models			
(T5.1)	$c_i \sim \text{Binomial}(N_i, \theta_i)$	(T5.1′)	$c_i \sim \text{Binomial}(N_i, \theta_i)$
Recapture models			
(T5.2)	$rm_i \sim \text{Hypergeometric}(N_i - x_i, m_i, r_i)$	(T5.2′)	$rm_i \sim \text{Binomial}(m_i, \theta_i)$
Likelihood for year i $L(N_i, \theta_i \mid d_i) = L_i$			
(T5.3)	$L_i = C_{N_i}^{c_i}\, \theta_i^{c_i} (1-\theta_i)^{N_i - c_i} \dfrac{C_{m_i}^{rm_i} C_{r_i - m_i}^{r_i - rm_i}}{C_{N_i - x_i}^{r_i}}$	(T5.3′)	$L_i = C_{N_i}^{c_i}\, \theta_i^{c_i} (1-\theta_i)^{N_i - c_i} C_{m_i}^{r_i}\, \theta_i^{m_i} (1-\theta_i)^{m_i - rm_i}$

Note: The subscript i indicates the year of migration; CMR data d_i for spawners are given in Table 3; c_i denotes the number of spawners caught at the upstream trap; x_i denotes the number of spawners that died during manipulation or that are removed for experimental use or hatchery production; m_i is the number of spawners marked and released ($m_i = c_i - x_i$); r_i is the recapture sample; and rm_i is the number of fish marked among r_i. CMR data d_i for smolts are given in Table 4; c_i denotes the number of smolts caught at the downstream trap; m_i is the number of smolts marked and released; and r_i is the number of marked recaptured. For spawners, N_i denotes the number of upstream migrating fish and q_i denotes the upstream trap efficiency. For smolts, N_i denotes the number of downstream migrating fish and q_i denotes the downstream trap efficiency. Notation $X \sim Z$ denotes that the variable X has the probability distribution Z. See text for details about the hypotheses underlying the model.

the requirement to derive by hand the full conditional distributions. It only requires the declaration of the full Bayesian model and the specification of the data. Model declaration consists of the deterministic equations linking the variables, the prior density of unknown variables, and the sampling distributions relating data and variables. Initial values for all unknowns are also needed to start the sampling process.

In any MCMC method, a critical issue is whether the simulated chain has converged to its ergodic target distribution. Following the recommendations of Spiegelhalter et al. (2000), we ran three different chains starting at contrasting initial values spread over the space of the unknown variables. We first ran the three MCMC chains for 5000 initial iterations. To diminish the effect of the starting points, these first 5000 iterations were considered a burn-in period and were discarded. We generated another 20 000 random draws to derive posterior inferences. We checked convergence of the chains using the Gelman and Rubin (1992) diagnostics as modified by Brooks and Gelman (1998) proposed by WinBUGS®. For most of the models fitted, Gelman–Rubin diagnostics indicated convergence for the three chains after those 20 000 iterations. For the others, we reran 20 000 or 40 000 additional simulations to obtain convergence.

The output after convergence of the MCMC chains consists of a joint sample from the posterior distribution of all unknowns of the model. The integration needed to derive the marginal posterior distribution of any subset of unknowns is straightforward. Indeed, the MCMC sample of the subset of interest is to be considered a sample from its marginal posterior distribution. We summarize marginal posterior distributions of interest by simple statistics directly computed from the MCMC samples: mean, median, and 95% Bayesian posterior credibility interval.

Results

Spawning run

Our results show that the inferences obtained under the ABM may be unreliable and highly sensitive to the choice of prior distributions. Posterior distributions of the θ_is and N_is derived from the ABM, with reference noninformative priors, vary highly between years in terms of both position and dispersion (Figs. 2*a*, 2*b*). The posterior estimates of the θ_is are particularly variable between years (Fig. 2*a*). However, the high dispersion of θ_is observed for years such as 1992 and 1993 does not necessarily have strong repercussion on the N_is (Fig. 2*b*). Years with very few adults caught at the trap are indicative of a low population size, as far as the recapture data allow discarding of very low trapping probabilities. Some years have precise and symmetric posterior distributions of N_i, whereas other years may conversely have highly dispersed and skewed posteriors (Fig. 2*b*). For the latter, the upper bounds of the 95% Bayesian credibility intervals appear unrealistically high given the size of the Oir River and the available knowledge on the biology and ecology of Atlantic salmon. Inferences on the N_is stem from the hypergeometric recapture experiments and thus depend on the recapture sample above all. Sparse mark–recapture data, i.e., low number of marked released or, more importantly, low number of recaptures of previously marked fish yield imprecise inferences (e.g., years 1987, 1990, and 1994). Posterior inferences under the ABM are rather robust to the choice of the prior on the θ_is. In contrast, posterior inferences on the N_is are highly sensitive to the prior choice. Changing the prior distribution of the N_is can have a strong influence on posterior distributions, especially for data-poor years (see Appendix A).

Hierarchical modeling greatly improves posterior inferences (Fig. 2): the most precise inferences are obtained under the HBM. It is the hierarchical structure on the N_is that is the major source of improvement. Compared with the ABM that assumes independence of both the N_is and the θ_is, the hybrid model assuming a hierarchical structure on the θ_is alone does not really improve the inferences on the variable of ultimate interest, N_i, and the sensitivity to the choice of the prior on the N_is is not alleviated (results not shown).

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Fig. 2. Spawners case. Marginal posterior distributions of (*a*) the θ_is (upstream trap efficiency) and (*b*) the N_is (number of upstream migrating fish) for years 1984 to 2000 obtained under four model structures. Line styles indicate the model investigated: solid line, hierarchical Bayesian model, with hyperpriors π_3 in Table A4 and π_2 in Table A5; broken line, hybrid model with hierarchical structure on the θ_is only with the hyperprior π_3 in Table A4, and the prior π_2 in Table A2 on the N_is with N_{max} = 2000; broken–dotted line, hybrid model with hierarchical structure on the N_is only with the hyperprior π_2 in Table A5 and the prior π_1 in Table A1 on the θ_is; dotted line, annual Bayesian model with the prior π_1 in Table A1 on the θ_is and the prior π_2 in Table A2 on the N_is with N_{max} = 2000. ▲ and ▼, 2.5 and 97.5 percentiles, respectively; ■, mean; +, median.

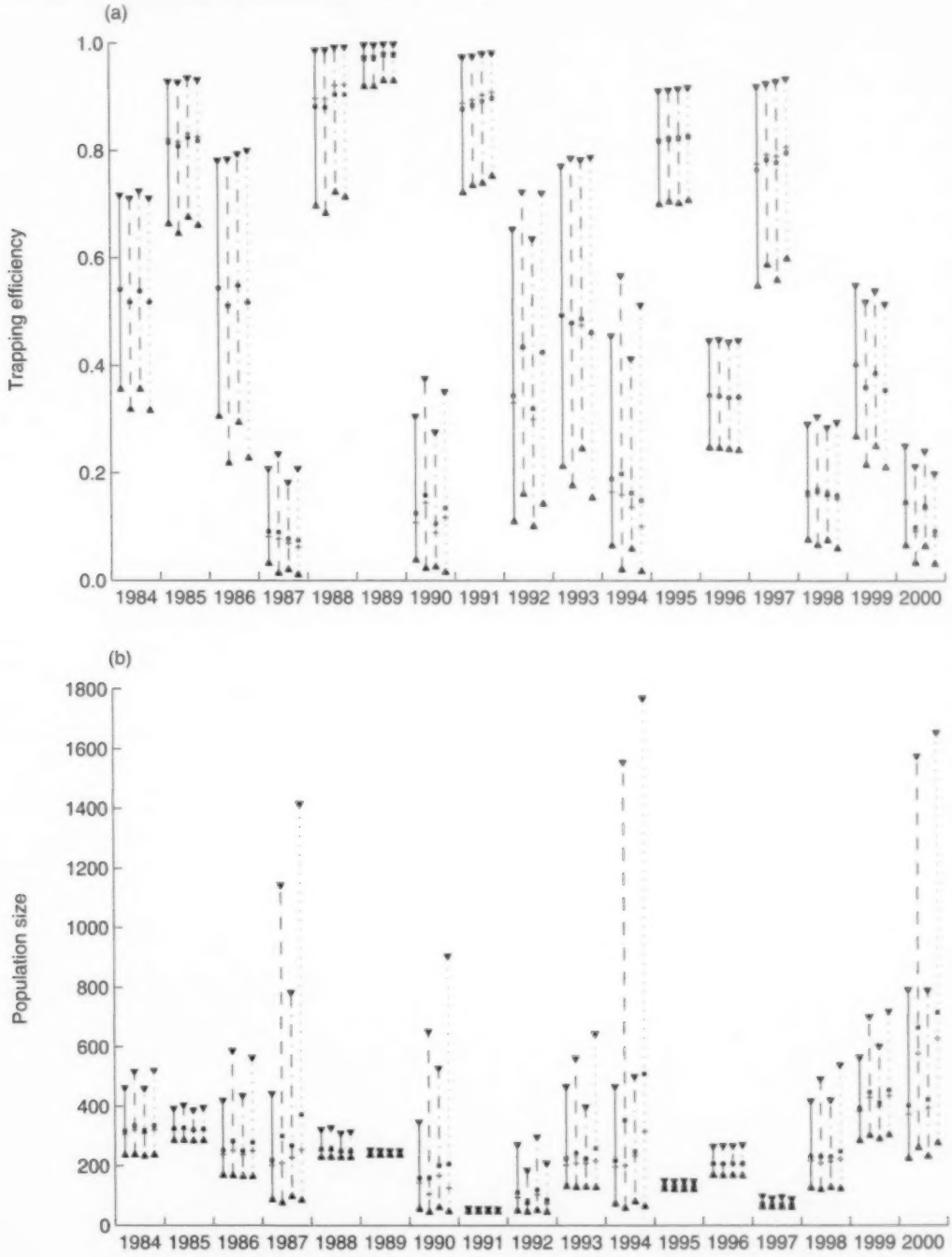

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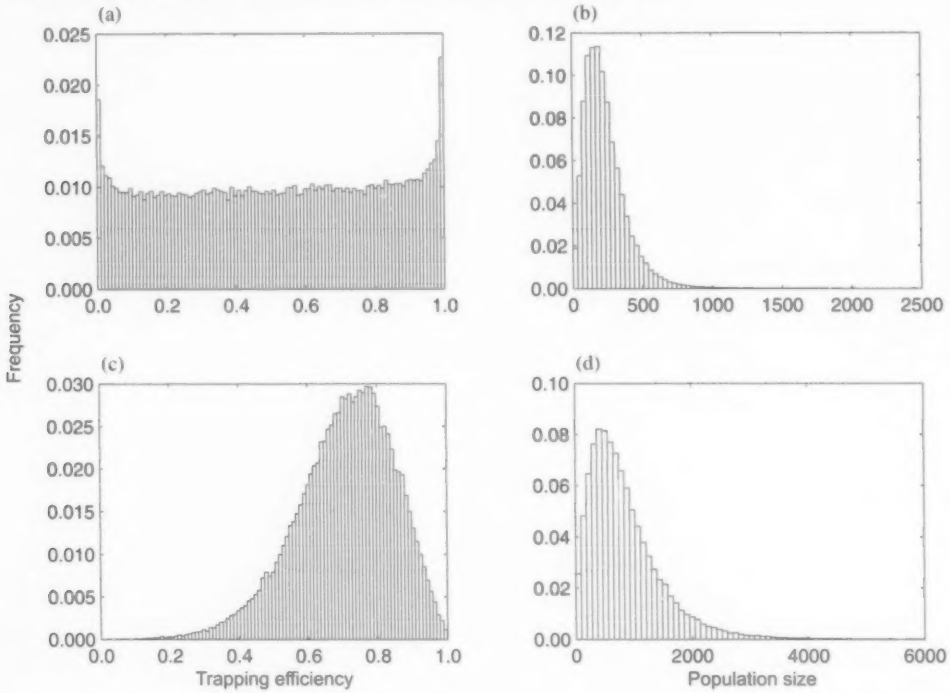
Fig. 3. Profiles of posterior predictive distributions $P(\tilde{\theta}|\text{data})$ and $P(\tilde{N}|\text{data})$ derived from the hierarchical Bayesian model in the spawners case (*a* and *b*, respectively) and in the smolts case (*c* and *d*, respectively). Hyperpriors used are π_3 in Table A4 and π_2 in Table A5. Profiles are frequency histograms issued from the Markov chain Monte Carlo samples.



Posterior mean values of the θ_is are only slightly shrunk toward the overall mean at around 0.5 (Fig. 2*a*). In contrast, setting a hierarchical structure on the N_is strongly reduces the skewness and uncertainty in the estimation of the N_is (Fig. 2*b*). The tails of the posterior distributions of the N_is are drastically shortened. These results appear much more sensible and realistic than those derived from the ABM. The reduction in uncertainty is particularly effective for years with poor CMR data. As expected, the gain in precision is insignificant for years with CMR data informative enough to enable precise estimation of the N_is under the ABM. Posterior inferences under the HBM are quite robust to the choice of priors for the hyperparameters (see Appendix A).

The posterior predictive of the mean trapping efficiency $P(\tilde{\theta}|\text{data})$, under the HBM (Fig. 3*a*), appears rather uninformative. The transfer of information between years for the trapping efficiencies is weak. This observation is consistent with the insignificant effect of setting a hierarchical structure on the θ_is. Unlike that of the trapping efficiency, the posterior predictive of the mean population size, $P(\tilde{N}|\text{data})$, is informative with a mean value around 230 and 95% of its density in the range [40,610] (Fig. 3*b*). The data of all years combined allow discarding a priori the possibility of very high spawner population size (i.e., greater than a thousand) in any additional year.

Smolt run

In contrast with the spawners case, the CMR data for the smolts appear to be much more informative and the ABM framework enables precise estimations that are quite robust to the prior choice. Posterior distributions of the θ_is are less variable between years than for spawners (Fig. 4*a*). The uncertainty around posterior estimates is generally much lower than in the spawners case. Posterior distributions of the N_is are also less dispersed and less skewed than for the spawners (Fig. 4*b*). Accordingly, the posterior inferences derived under the ABM are rather insensitive to the choice of priors (see Appendix A).

Unlike in the spawners case, the HBM does not significantly improve posterior inferences compared with the ABM (Fig. 4). The hierarchical structure has more effect on posterior inferences for θ_is than for N_is. The hierarchical structure on θ_i has a slight shrinkage effect that reduces between-year variation (Fig. 4*a*): the most extreme estimates of θ_i are barely pulled up to the values of the other years (e.g., 1990, 1993, 1994, 1997, and 1998). Posterior distributions of N_is and θ_is under the HBM are robust to the choice of priors for the hyperparameters (see Appendix A).

In contrast with the spawners, both the posterior predictive $P(\tilde{\theta}|\text{data})$ and $P(\tilde{N}|\text{data})$ for the smolts are informative (Figs. 3*c*, 3*d*). On the basis of the data collected from 1986 to 2001, the probability of capture at the smolt trap is expected to average 0.7 with a 95% posteriori credibility interval [0.39,0.94]. The smolt run is expected to have 95% probability of being in the range [90,2500] with a mean of 850. However, the transfer of information between years remains of little use because yearly data are always informative enough.

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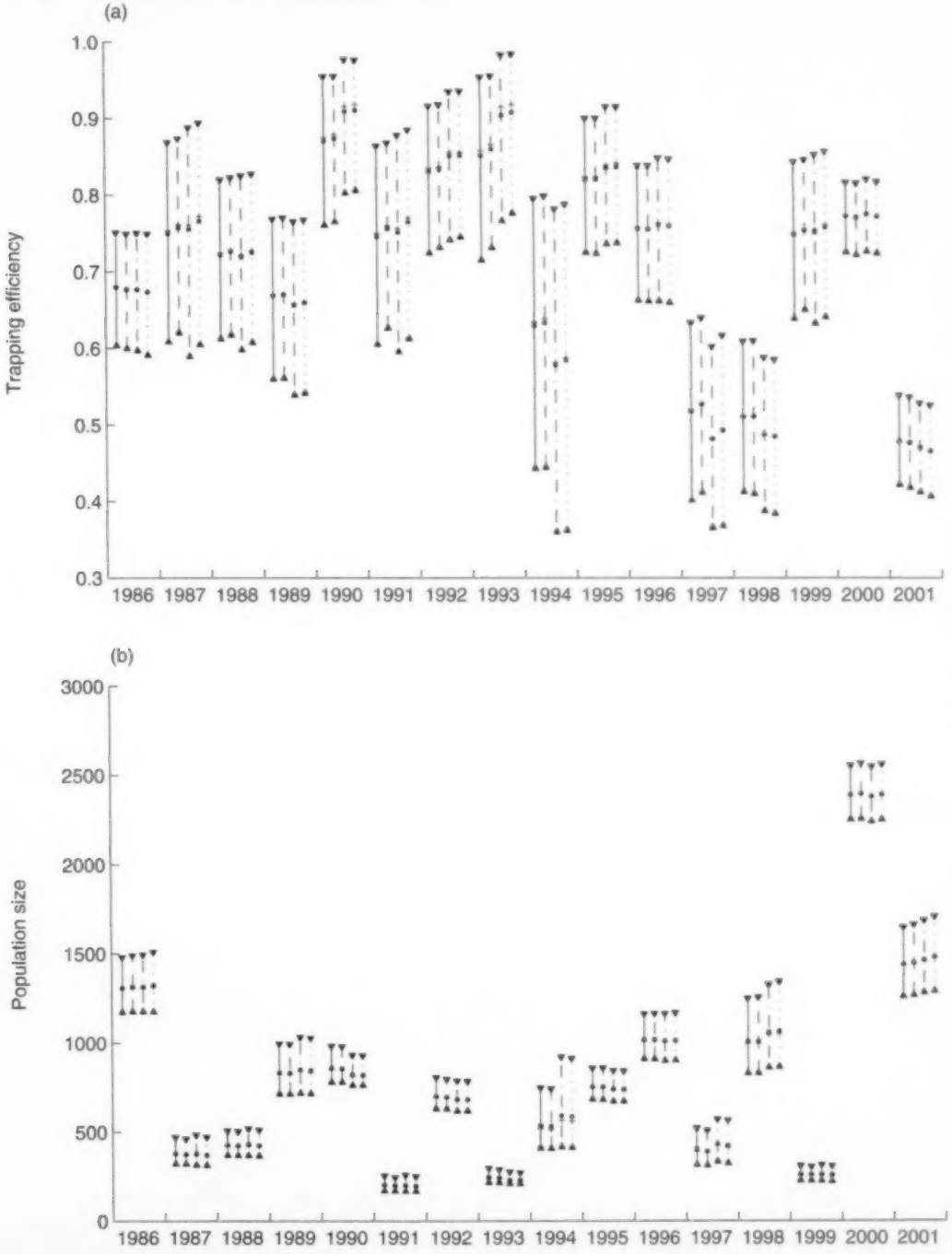
Fig. 4. Smolts case. Marginal posterior distributions of (*a*) the θ_js (downstream trap efficiency) and (*b*) the N_js (number of downstream migrating fish) for years 1986 to 2001 obtained under four model structures. Line styles indicate the model investigated: solid line, hierarchical Bayesian model, with hyperpriors π_3 in Table A4 and π_2 in Table A5; broken line, hybrid model with a hierarchical structure on the θ_js only with the hyperprior π_3 in Table A4, and the prior π_2 in Table A2 on the N_js with $N_{max} = 4000$; broken–dotted line, hybrid model with hierarchical structure on the N_js only with the hyperprior π_2 in Table A5 and the prior π_1 in Table A1 on the θ_js; dotted line, annual Bayesian model with the prior π_1 in Table A1 on the θ_js and the prior π_2 in Table A2 on the N_js with $N_{max} = 4000$. ▲ and ▼, 2.5 and 97.5 percentiles, respectively; ■, mean; +, median.



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Discussion

Assessment of founding hypotheses

Like any model for a CMR experiment, our approach relies on the agreement with the classical hypotheses H1–H4 and H1′–H4′ (see Materials and methods section). Warren and Dempson (1995), Arnason et al. (1996), and Schwarz and Taylor (1998) discussed how some of those hypotheses can be relaxed without strong consequences on the population size estimates. However, departure from those hypotheses may yield inaccurate estimates. Stratified models accounting for nonconstant catchability over time or heterogeneity in the capture probability between individuals may be more appropriate than pooled models (Pollock 1981, 1991; Plante et al. 1998). They have been applied to estimate Atlantic salmon migrations (Dempson and Stansbury 1991) or Pacific salmon migrations (Schwarz and Dempson 1994; Miyakoshi and Kudo 1999; Newcomb and Coon 2001). However, in many instances, as in our illustrative case study, the detailed information required to fit those models is not available and pooling is necessary. The robustness of pooled models to the departure from their underlying hypotheses is beyond the scope of this paper, which focuses on the contribution of hierarchical modeling. Yet, it is worth keeping in mind that some hypotheses may be questionable.

Hierarchical modeling can significantly improve inferences

Our paper is focused on the comparative merits of HBM versus ABM in the estimation of the quantities of interest and primarily the N_is. Formal statistical procedures, e.g., the deviance information criteria (DIC; Spiegelhalter et al. 2002), may provide some valuable indication for selecting the most appropriate model. However, we followed Spiegelhalter et al. (2002) in believing that such a formal selection approach could be of little relevance when other features of the models can be taken into account. We thus preferred to found the comparison between the models on two main criteria: the dispersion of posterior inferences of quantities of ultimate interest, i.e., the N_is, and the sensitivity to the choice of prior.

In the spawners case, the HBM clearly yields more reliable inferences compared with the ABM. However, the hybrid model assigning the θ_is a common hierarchical distribution while letting the N_is be independent only slightly modifies the inferences when compared with the ABM. The yearly CMR data indicate that θ_is have little in common between years. This is probably because they are influenced by the water discharge during the migration season. In this case, the hierarchical hypothesis on θ_is has no effect because there is very little information transferred among years through the hyperparameters γ. The spread of the posterior distribution of γ remains wide. As a consequence, the marginal prior on θ_is is as diffuse as if θ_is were assigned independent uninformative priors, and subsequent inferences are not markedly different.

A noticeable positive effect is obtained by imposing a hierarchical structure on N_is. The spawners CMR data set typifies a survey where data are poor for some years. Inferences on the N_is based on the ABM are of little reliance when the number of marks released or the size of the recapture sample are too small. Consequently, posterior distributions of estimates are widely dispersed, and some 95% posterior credibility intervals may spread over ecologically unrealistic values. Another detrimental effect is high sensitivity to the prior choice because the data do not contain sufficient information to dominate the prior. For certain years, two prior distributions, both meant to be uninformative, yield markedly different posterior estimates of N_is (see Appendix A). Several studies have already highlighted such sensitivity (Raftery 1988; Smith 1991; Garthwaite et al. 1995). Inferences on N_is are also sensitive to minor changes in the data (Chao 1989) and consequently may be nonrobust to errors made when collecting data. Thanks to its ability to take advantage of the whole historical information available, the HBM limits these undesirable effects and significantly improves the inferences. The posteriors of the N_is are less dispersed, more coherent, and more robust to changes in the prior assumptions. In the HBM, the posterior distribution of each year in turn is obtained by the combination of the likelihood with a modified prior that uses the data from all other years. This modified prior is informative about the N_is and the information that it brings is significant compared with that of a single year with poor data.

In contrast with the spawners case, fitting the HBM to the smolts data does not significantly improve inferences on the N_is compared with the ABM. The hierarchical structure on both θ_is and N_is has no effect because the likelihood always dominates the prior. Indeed, unlike in the spawners case, the yearly CMR data for smolts are highly informative. The information brought by all years combined is negligible compared with that of any single year. Consequently, the use of a noninformative prior, as in the ABM, or of an informative prior based on historical information, as in the HBM, makes little difference.

The contrasted results obtained for the spawners and the smolts shows that the contribution of the hierarchical modeling is positive or null. In the best case, setting a hierarchical structure improves the inferences; in the worst case, it remains neutral.

General interest of the hierarchical approach to the analysis of ecological data

We believe that hierarchical Bayesian modeling has a great potential of application in the analysis of ecological data. The interesting properties revealed by our specific study could be extended to many cases considering a collection of units in time or space, yet partial commonality can be assumed across units. Whenever there are enough units to derive posterior inferences about the hyperparameters, we encourage the use of an exchangeable hierarchical model.

Hierarchical modeling is almost universally applicable even when some available knowledge would prevent the similarities and (or) differences between units from being modeled as draws from a common probability distribution. Indeed, any information available to distinguish different units can be encoded in covariates and accounted for in a conditional independent model, which assumes partial exchangeability (Gelman et al. 1995). In our case, it might have been possible to model the variations of θ_is with the water discharge, Q_i, by any function of the form $\theta_i = f(Q_i) + \varepsilon_i$, where ε_is are random residuals. The partial exchange-

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ability can be invoked by assuming that ε_is are exchangeable with hyperparameters Ψ. Exchangeability is then modeled by the conditional independence in eq. 3:

$$(3) \qquad \pi(\theta|Q_1,\ldots,Q_I, \psi) = \pi(\psi)\prod_{i=1}^{I}\pi(\theta_i|Q_i, \psi)$$

The analysis of data in a hierarchical framework is now simplified by the use of MCMC algorithms within modern software such as WinBUGS®. Sensitivity analysis of posterior inferences to the choice of priors is also facilitated. George and Robert (1992) already showed that CMR models lend themselves to Bayesian treatment using the Gibbs sampler. However, they faced the practical restrictions that the prior and the likelihood must lead to conditional posterior distributions, which are easily amenable to simulations. WinBUGS® allows for a wide choice of prior and sampling distributions, even if they lead to highly nonstandard conditional posteriors (Gentleman 1997; Meyer and Millar 1999). Formulations that would have been avoided in the past because of analytical and numerical difficulties can now be easily considered for practical applications. Prior and sampling distributions can be modified without having to respecify analytically the full conditional probability distributions and without getting bogged down by details about the densities used.

Because of the transfer of information between years, a hierarchical framework can accommodate missing data, provided they are few. In our example concerning smolts, let us imagine that recapture data is missing for a particular year i. Even in the absence of yearly data to update θ_i, the prior $\pi(\theta_i)$ will be updated by the data of all years except i, i.e., data_i^*. This "updated" informative prior allows us to derive more precise posterior inferences on N_i than the initial prior $\pi(\theta_i)$.

To conclude, an exchangeable hierarchical model appears as a superior methodology to treat many ecological data sets. As we pointed out, a model that considers each unit independently may be considered a particular case of an exchangeable hierarchical model. When the data set contains poorly informative or even missing data, the independence assumption between the sampling units may lead to widely dispersed posterior inferences. To reduce uncertainty, one may be tempted to use informative priors. However, this generally consists of adapting the prior to the amount of information brought by the data, e.g., the less informative the data, the more informative the prior introduced. This may result in the observations playing a role in determining the prior distribution, and this practice must be strongly discouraged. We encourage others to consider a hierarchical model as the default choice. As noted by Gelman et al. (1995), even if the unknown variables to estimate vary highly among units, it is not irrelevant to estimate them in a hierarchical framework. For each unit, an updated prior is build by combining information from all experiments in a consistent and parsimonious framework. This informative prior is scaled to the between-units (e.g., years in our case study) variability and each unit's contribution is judiciously weighed, i.e., depending on how informative its corresponding data are. The inferences about quantities of interest can be significantly improved in terms of both precision and robustness to the choice of prior distributions on hyperparameters.

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Appendix A

Specification of the priors and sensitivity analysis

To investigate the robustness of our conclusions to the choice of priors, we compared posterior distributions obtained with several priors with various mean and dispersion features, either informative or not. We first give the distribution that we tested in the annual Bayesian model (ABM) for both the θ_is and the N_is (Tables A1 and A2). Then, we describe the conditional prior distributions $\pi(\theta_i|\gamma)$ and $\pi(N_i|\delta)$ (Table A3) and the diffuse hyperpriors on γ and δ (Tables A4 and A5). Almost all of the priors that we used for the N_is in the ABM and for hyperparameters in the hierarchical Bayesian model (HBM) are bounded. By restricting the priors to a finite domain of variation, we ensure that all priors are proper. We thereby avoid improper posterior distributions that may arise from the use of improper priors (Gelman et al. 1995). In the HBM, the ranges used for the hyperparameters were taken wide enough that the posterior mass was not accumulated close to the bounds and that increasing the range did not affect the posterior distributions. We thus ensured that we did not affect a priori null density to a domain where the likelihood was non-null.

Table A1. Prior distributions for the θ_is used in the ABM for both spawners and smolts.

$\pi_1(\theta_i) \sim$ Beta(½,½)
$\pi_2(\theta_i) \sim$ Beta(1,1)
$\pi_3(\theta_i) \sim$ Beta(0.01,1)
$\pi_4(\theta_i) \sim$ Beta(1,0.01)

ABM: prior on the θ_is (Table A1)

Beta distributions were assigned to the θ_is. The Beta distribution allows very different shapes and is the natural conjugate for the classical Binomial likelihood (Box and Tiao 1992). We tested four different sets for the hyperparameters (α,β) that reflect different prior opinion. Setting $\alpha = \beta$ in π_1 and π_2 yields symmetric distribution around 0.5. π_1 is the standard noninformative prior (Box and Tiao 1992), and π_2 corresponds to a Uniform on [0,1] (used by Raftery 1988). π_3 and π_4 give strong weight to values of θ_i close to 0 and close to 1, respectively. π_3 is closed to an improper prior $\propto 1/\theta_i$ used as a noninformative by Garthwaite et al. (1995) for their multicapture–recapture census model.

ABM: prior on the N_is (Table A2)

We first tested different discrete little informative priors. They are adapted to situations where only vague prior knowledge about the N_is is available and when the aim is to extract the useful information from the data. The bounded Uniform discrete prior π_1 is motivated by its practical convenience (used by Gazey and Staley 1986 or Chao 1989). The only information that it brings into the analysis is that a zero probability is assigned to values greater than the truncation point N_{max}. The classical discrete prior π_2 is used as an uninformative prior by Raftery (1988), Smith (1991), George and Robert (1992), and Garthwaite et al. (1995). For both π_1 and π_2, we assessed the sensitivity of the posterior inferences to the choice of the bound by testing different values of N_{max}.

To avoid the subjective choice of the bounds, we also tried the Inverse Binomial (or Negative Binomial) as a robust alternative to the Poisson law proposed by Raftery (1988). As suggested by Smith (1991), we used a two-step prior density to simulate the Inverse Binomial. If the conditional distribution of N_i is considered to be Poisson with mean λ, and if λ has the natural conjugate distribution Gamma(a,b), then the unconditional distribution of N_i is Inverse Binomial with parameters (a,b) (see Raftery 1988 or Smith 1991). We first

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Table A2. Prior distributions for the N_is used in the ABM.

	Form	Bounds or parameters	
		Spawners	Smolts
$\pi_1(N_i)$	Uniform on $[0,N_{max}]$	N_{max} = 1000,2000,3000	N_{max} = 4000,7000,10 000
$\pi_2(N_i)$	$1/N$ on $[1,N_{max}]$	N_{max} = 1000,2000,3000	N_{max} = 4000,7000,10 000
$\pi_3(N_i)$	Poisson(λ)	λ ~ Inverse Gamma(0.001,0.001)	λ ~ Inverse Gamma(0.001,0.001)
$\pi_4(N_i)$	Inverse Binomial(a,b)	(E_N,σ_N) = (100,20)	(E_N,σ_N) = (1500,300)

Note: For both spawners and smolts, (E_N,σ_N) values are grounded on previous knowledge gathered on a nearby river, the Scorff River (Brittany) (see Baglinière et al. 1993 for the smolts and Prévost 2000 for the spawners).

Table A3. Beta and Inverse Binomial conditional prior distributions for θ_i and N_i (Gelman et al. 1995).

Beta distribution for θ_i

For all i in 1,...,I

$$\text{(TA3.1)}\quad \pi(\theta_i|\alpha,\beta)=\frac{\Gamma(\alpha+\beta)}{\Gamma(\alpha)\Gamma(\beta)}\theta_i^{\alpha-1}(1-\theta_i)^{\beta-1},\qquad \alpha>0,\beta>0,\theta_i\in[0,1]$$

Mean and variance

$$\text{(TA3.2)}\quad \begin{cases} E_\theta(\alpha,\beta)=\dfrac{\alpha}{\alpha+\beta} \\ V_\theta(\alpha,\beta)=\dfrac{\alpha\beta}{(\alpha+\beta)^2(\alpha+\beta+1)} \end{cases}$$

Inverse transformation under the constraint $V_\theta < E_\theta(1 - E_\theta)$

$$\text{(TA3.3)}\quad \begin{cases} \alpha(E_\theta,V_\theta)=E_\theta\left(\dfrac{E_\theta(1-E_\theta)}{V_\theta}-1\right) \\ \beta(E_\theta,V_\theta)=(1-E_\theta)\left(\dfrac{E_\theta(1-E_\theta)}{V_\theta}-1\right) \end{cases}$$

Inverse Binomial distribution for N_i

For all i in 1,...,I

$$\text{(TA3.4)}\quad \pi(N_i|a,b)=C_{N_i+a-1}^{a-1}\left(\frac{b}{b+1}\right)^a\left(\frac{1}{b+1}\right)^{N_i},\qquad a>0,b>0,N_i=0,1,\ldots$$

Mean and variance

$$\text{(TA3.5)}\quad \begin{cases} E_N(a,b)=\dfrac{a}{b} \\ V_N(a,b)=\dfrac{a(b+1)}{b^2} \end{cases}$$

Inverse transformation under the constraint $V_N > E_N$

$$\text{(TA3.6)}\quad \begin{cases} a(E_N,V_N)=\dfrac{{E_N}^2}{(V_N-E_N)} \\ b(E_N,V_N)=\dfrac{E_N}{(V_N-E_N)} \end{cases}$$

Table A4. Priors on the natural hyperparameters $\gamma = (\alpha,\beta)$ or transformed ones used in the HBM for both spawners and smolts.

	Parameters	Form	Bounds
π_1	Initial (α,β)	Uniform on $[\alpha_{min},\alpha_{max}] \times [\beta_{min},\beta_{max}]$	$[\alpha_{min},\alpha_{max}]$ = [0,100] $[\beta_{min},\beta_{max}]$ = [0,100]
π_2	$u = \ln(\alpha/\beta)$ $v = \ln(\alpha + \beta)$	Uniform on $[u_{min},u_{max}] \times [v_{min},v_{max}]$	$[u_{min},u_{max}]$ = [−5,10] $[v_{min},v_{max}]$ = [−5,10]
π_3	(E_θ,V_θ)	E_θ ~ Beta(½,½) $V_\theta\|E_\theta \propto 1/V_\theta$ on $[V_{\theta\,min},V_{\theta\,max}\|E_\theta]$	$V_{\theta\,min} = 1 \times 10^{-20}$ $V_{\theta\,max}\|E_\theta = E_\theta(1 - E_\theta)$

used the unbounded uninformative (improper) prior π_3 obtained when λ has an improper prior distribution proportional to $1/\lambda$. Practically, we approximated this distribution by first drawing λ from an Inverse Gamma(0.001,0.001) (see Meyer and Millar 1999 or Su et al. 2001). π_4 reflects subjective information about the N_is. A priori informative

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Fig. A1. Spawners case. (*a*) Sensitivity analysis of marginal posterior distributions of the θ_ts to the choice of the prior on the θ_ts in the annual Bayesian model (ABM). Line styles indicate the four priors on the θ_ts investigated (Table A1): solid line, π_1; broken line, π_2; dotted line, π_3; broken–dotted line, π_4. Prior used on the N_ts is π_2 in Table A2 with N_{max} = 2000. (*b*) Sensitivity analysis of marginal posterior distributions of the N_ts to the choice of the prior on the N_ts in the ABM. Line styles indicate the four priors on the N_ts investigated (Table A2): solid line, π_1 with N_{max} = 2000; broken line, π_2 with N_{max} = 2000; dotted line, π_3; broken–dotted line, π_4. Prior used on the θ_ts is π_1 in Table A1. ▲and ▼, 2.5 and 97.5 percentiles, respectively; ■, mean; +, median.

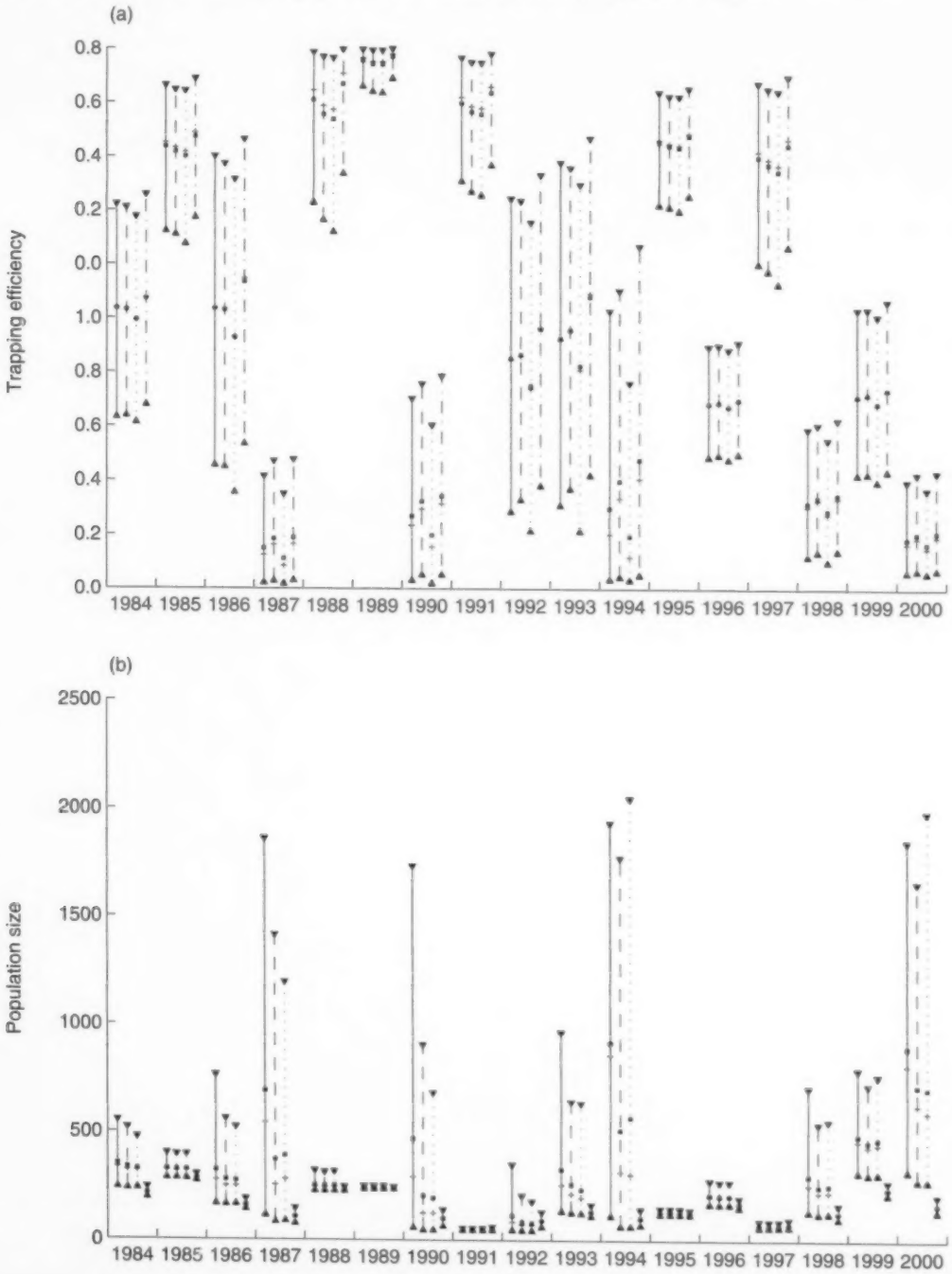

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Fig. A2. Smolts case. (*a*) Sensitivity analysis of marginal posterior distributions of the θ_is to the choice of the prior on the θ_is in the annual Bayesian model (ABM). Line styles indicate the four priors on the θ_is investigated (Table A1): solid line, π_1; broken line, π_2; dotted line, π_3; broken–dotted line, π_4. Prior used on the N_is is π_2 in Table A2 with $N_{max} = 4000$. (*b*) Sensitivity analysis of marginal posterior distributions of the N_is to the choice of the prior on the N_is in the ABM. Line styles indicate the four priors on the N_is investigated (Table A2): solid line, π_1 with $N_{max} = 4000$; broken line, π_2 with $N_{max} = 4000$; dotted line, π_3; broken–dotted line, π_4. Prior used on the θ_is is π_1 in Table A1. ▲ and ▼, 2.5 and 97.5 percentiles, respectively; ■, mean; +, median.

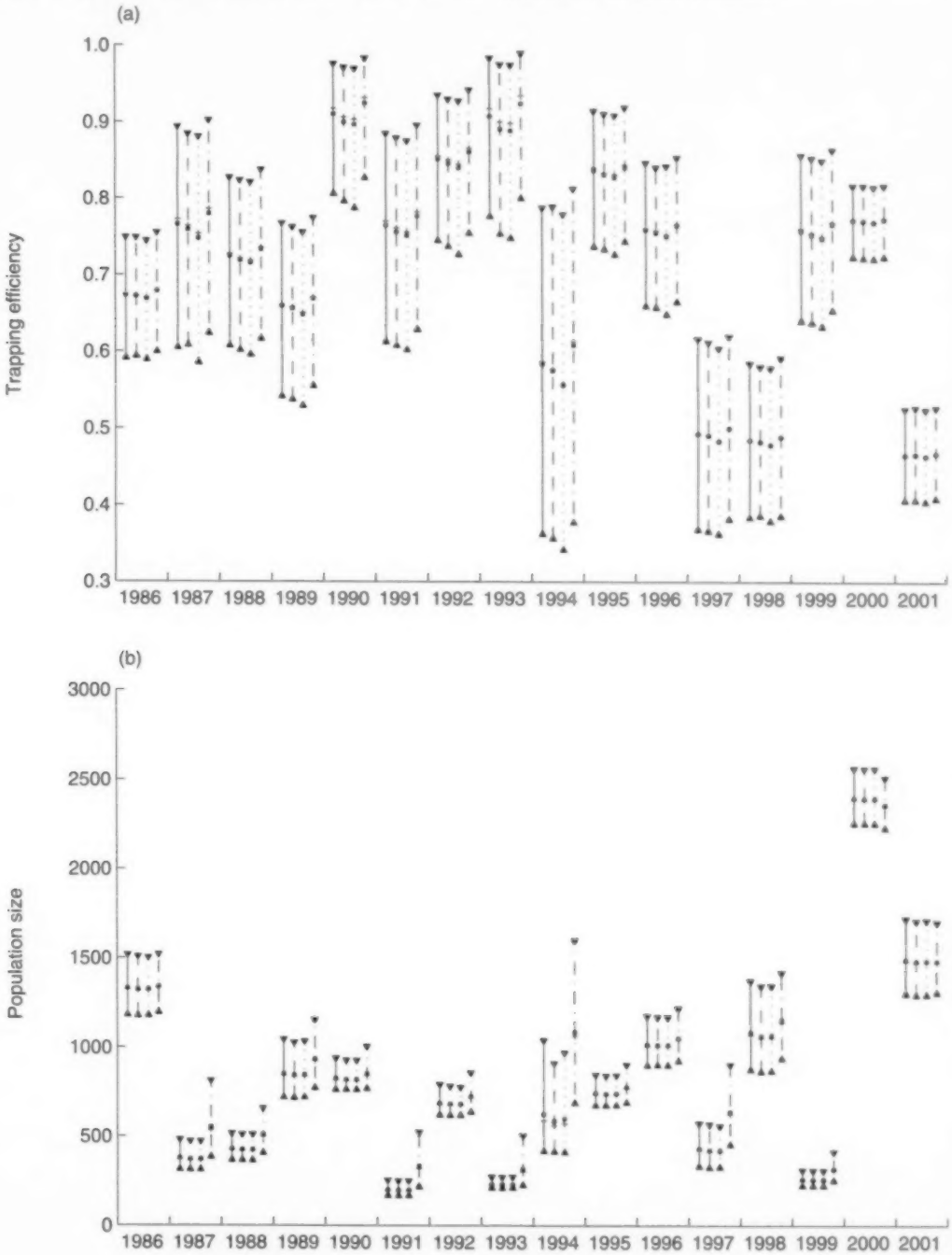

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Table A5. Priors on the natural hyperparameters $\delta = (a,b)$ or transformed ones used in the HBM for both spawners and smolts.

	Parameters	Form	Bounds
π_1	Initial (a,b)	Uniform on $[a_{min},a_{max}] \times [b_{min},b_{max}]$	$[a_{min},a_{max}] = [0,50]$; $[b_{min},b_{max}] = [0,50]$
π_2	(E_N,V_N)	$E_N \sim$ Uniform on $]0,E_{N\,max}[$; $V_N \mid E_N \propto 1/V_N$ on $]E_N,V_{N\,max}[$	$E_{N\,max} = 6000$; $V_{N\,max} = 1.0 \times 10^6$

values are chosen for E_N and σ_N, the mean and standard deviation for the N_is. To determine the corresponding (a,b) parameters of the Inverse Binomial, we use the inverse transformation between the mean and standard deviation and the natural parameters in TA3.5.

HBM: conditional priors $\pi(\theta_i|\gamma)$ and $\pi(N_i|\delta)$ and hyperpriors $\pi(\gamma)$ and $\pi(\delta)$

In the HBM, the natural choice for the conditional prior distributions $\pi(\theta_i|\gamma)$ and $\pi(N_i|\delta)$ are the Beta and the Inverse Binomial distributions, respectively, in Table A3. The parameters for which a prior distribution must be specified are the hyperparameters of the Beta and Inverse Binomial, denoted $\gamma = (\alpha,\beta)$ and $\delta = (a,b)$, respectively. These are higher level parameters and are generally assigned a diffuse hyperprior distribution to reflect our ignorance about them. As posterior inferences may be sensitive to the hyperpriors, we also compared results obtained with several hyperpriors $\pi(\gamma)$ and $\pi(\delta)$, which illustrate different interpretations of our little knowledge a priori (Tables A4 and A5).

Hyperprior $\pi(\gamma)$ (Table A4)

Different forms intended to reflect vague prior information about the capture probability have been proposed by Gelman et al. (1995), George and Robert (1992), and Smith (1991). The simplest that we tested is π_1, a bounded Uniform distribution on the initial Beta parameter (α,β). Instead of defining a prior directly on (α,β), it could be relevant to set a prior on some appropriate one-to-one transformed parameters and then to go back to (α,β) via the inverse transformation. π_2 considers a bounded Uniform on the transformed parameters $(\log(\alpha/\beta),\log(\alpha + \beta))$ (Gelman et al. 1995). π_3 is a noninformative on (E_θ,V_θ), respectively the mean and variance of the Beta distribution. The equations TA3.3 give the one-to-one relationship of (α,β) in terms of (E_θ,V_θ). To ensure that the parameters (α,β) are >0, V_θ must satisfy the constraint $V_\theta < E_\theta(1 - E_\theta)$. Practically, to simulate π_3, we use a two-step conditional prior density. We first draw E_θ in a Beta(½,½). Then, to respect the previous constraint, we draw V_θ in a noninformative prior $\propto 1/V_\theta$ over the restricted range $[V_{\theta\,min}, E_\theta(1 - E_\theta)]$ conditioned on the value E_θ previously drawn.

Hyperprior $\pi(\delta)$ (Table A5)

The prior distribution π_1 is a bounded Uniform on initial parameters (a,b). π_2 corresponds to a noninformative prior on (E_N,V_N), respectively the mean and variance of the Inverse Binomial distribution. Equation TA5.6 gives the expression of (a,b) in terms of (E_N,V_N). To simulate π_2, we used a two-step conditional prior density as for $\pi_3(E_\theta,V_\theta)$. We assigned a bounded Uniform distribution over $]0,E_{N\,max}[$ to E_N. To ensure that (a,b) are positive, we draw V_N in a prior $\propto 1/V_N$ over the range $]E_N,V_{N\,max}[$.

Results of the sensitivity analysis

Spawning run

Posterior distributions of the θ_is in the ABM are slightly sensitive to the choice of the prior $\pi(\theta_i)$ (Fig. A1*a*, Table A1). This sensitivity has only moderate repercussions on the posterior of the N_is (results not shown). By contrast, changing prior distribution on the N_is in the ABM (Table A2) has strong influence on posterior estimations (Fig. A1*b*). Two priors, both meant to be uninformative (π_1 and π_2, Table A2), yield markedly different estimates. Moreover, both π_1 and π_2 (Table A2) lead to very skewed posteriors with tails that are sensitive to the choice of the truncation point N_{max} (results not shown). Sensitivity to the prior is especially acute for data-poor years (i.e., 1987, 1990, 1994). For these years, an informative prior such as π_4 (Table A2) dominates the likelihood, thus leading to markedly different results than vague priors. Posterior inferences derived under the HBM are robust to the choice of priors on hyperparameters (Tables A4 and A5) (results not shown).

Smolt run

Unlike in the spawners case, the results obtained in the ABM are rather robust to the choice of prior. The sensitivity to the choice of the prior on the θ_is is slight (Fig. A2*a*) and has hardly any repercussion on the posterior inferences on the N_is (results not shown). The influence of the priors on the N_is is much less important than for spawners. The three different diffuse priors π_1, π_2, and π_3 (Table A2) yield similar posterior distributions (Fig. A2*b*). We have not detected any significant sensitivity to the choice of the bounds N_{max} for π_1 and π_2 in Table A2 (results not shown). The likelihood always dominates the prior, even when the informative prior is used (π_4 in Table A2). Posterior inferences are robust to the choice of priors on hyperparameters (Tables A4 and A5) (results not shown).

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A size-based model of the impacts of bottom trawling on benthic community structure

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Abstract: Bottom trawling causes widespread disturbance to the sediments in shallow-shelf seas. The resultant mortality of benthic fauna is strongly size dependent. We empirically demonstrate that beam trawling frequency in the central North Sea had a greater effect on fauna size distribution in a soft sediment benthic community than variables such as sediment particle size and water depth. Accordingly, we simulated the impacts of trawling disturbance on benthos using a model consisting of 37 organism size classes between 1 μg and 140 g wet weight. The model produced a production–biomass versus size relationship consistent with published studies and allowed us to predict the impacts of trawling frequency on benthos size distributions. Outputs were consistent with empirical data; however, at high yet realistic trawling frequencies, the model predicted an extirpation of most macrofauna. Empirical data show that macrofauna persist in many heavily trawled regions: therefore, we suggest that trawling by real fisheries is sufficiently heterogeneous to provide spatial refuges less impacted by trawling. If correct, our analyses suggest that fishery management measures that do not reduce total effort but do lead to effort displacement and spatial homogenization (e.g., temporarily closed areas) may have adverse effects on the systemic persistence of intermediate- and large-sized macrofauna.

Résumé : Le chalutage de fond cause une perturbation importante des sédiments dans les mers peu profondes du plateau continental. Nous démontrons de façon empirique que la fréquence de chalutage à perche dans la région centrale de la mer du Nord a un effet plus prononcé sur la distribution de fréquence des tailles de la faune dans une communauté benthique sur sédiments mous que des variables telles que la taille des particules des sédiments et la profondeur de l'eau. C'est pourquoi, nous avons simulé les impacts de la perturbation due au chalutage sur le benthos à l'aide d'un modèle qui comprend 37 classes de taille d'organismes, allant de 1 μg à 140 g de masse humide. Le modèle génère une relation entre la production/biomasse et la taille qui est compatible avec les données publiées et il nous permet de prédire les impacts de la fréquence de chalutage sur la distribution de fréquence des tailles du benthos. Les résultats du modèle sont compatibles avec les données empiriques; cependant, à des fréquences élevées, mais réalistes, de chalutage, le modèle prédit l'élimination de presque toute la macrofaune. Les données empiriques indiquent que la macrofaune persiste dans plusieurs des régions de chalutage intense; ainsi, nous croyons que le chalutage dans des conditions réelles de pêche est suffisamment hétérogène pour laisser des refuges spatiaux qui sont moins affectés. Si elles sont exactes, nos analyses laissent croire que les mesures de gestion des pêches qui ne réduisent pas l'effort total de pêche, mais qui mènent au déplacement de cet effort et à une homogénéisation spatiale (e.g. des régions fermées temporairement) peuvent avoir des effets négatifs sur la persistance systémique de la macrofaune de taille intermédiaire et grande.

[Traduit par la Rédaction]

Introduction

Trawling disturbance has wide-ranging impacts on the diversity, structure, and productivity of benthic communities (Dayton et al. 1995; Jennings and Kaiser 1998; Hall 1999). Knowledge of these impacts is based primarily on empirical studies that describe biological differences among communities subject to different levels of trawling disturbance (Thrush et al. 1998; Collie et al. 2000; Kaiser et al. 2000). Such studies are essential for understanding trawling impacts; however, future demands on science will be for quantitative methods predicting changes in communities resulting from trawling. An improved understanding of mechanisms would help to this end by describing how changing patterns and intensities of trawling disturbance affect benthic communities.

At least two factors must be considered when examining effects of trawling on benthic populations: the immediate mortality inflicted by trawling gear and the longer-term ability of populations to cope with this mortality. As both of these processes are functions of body size, size-based models are likely to provide a useful framework to examine questions concerning impacts of trawling activities on the

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entire benthic community rather than smaller studies on one or a few species.

Trawling leads to the mortality of benthic invertebrates because they are crushed directly by the trawl, exposed to predators by the passage of the trawl, or are caught in the net and die after capture and return to the sea (Ramsay et al. 1997; Bergman and van Santbrink 2000*a*, 2000*b*). Within and among species, the mortality rates suffered by the smallest individuals may be lower because they may be pushed aside by the pressure wave in front of the trawl (Gilkinson et al. 1998). Larger individuals usually suffer higher mortality if they are in the path of the trawl, although actual mortality rates are dependent on their distribution in the sediment. Thus, deeper-burrowing individuals may not come into contact with fishing gear because trawls rarely penetrate more than 6 cm into sand–mud sediments (Lindeboom and de Groot 1998; Bergman and van Santbrink 2000*a*, 2000*b*). Burrowing depth may increase with body size for some bivalves (Zaklan and Ydenberg 1997), and so larger individuals may be less vulnerable to mortality. Despite the trawling mortality refuge for some large individuals and observations of decreased mortality relative to intermediate-sized species (Bergman and van Santbrink 2000*a*, 2000*b*), large species usually show the greatest decreases in abundance following chronic (long-term) trawling disturbance. This is because large body size is correlated with slower growth, lower annual reproductive output, and lower intrinsic rates of natural increase (Charnov 1993; Brey 1999). Thus populations of large species, despite suffering lower mortality, may be less able to withstand these mortality rates than populations of smaller species.

In recent years, fishery managers have been asked to account for the ecosystem effects of fishing when formulating management plans (e.g., Ecosystem Principles Advisory Panel 1999). Trawling effects on benthic communities are a key concern because they may affect food availability for commercial fishes, modify food webs, and reduce diversity (Rijnsdorp and Millner 1996; Rijnsdorp and van Leeuwen 1996; Jennings and Kaiser 1998). Although we know many impacts of trawling from several studies, managers lack quantitative tools that allow them to predict the responses of benthic communities to changes in the intensity and distribution of trawling disturbance. Changes in the intensity and distribution of disturbance could result from catch or effort controls or technical measures such as the imposition of a closed area; hence, a quantitative predictive capacity is needed to assess the implications and efficacy of such management actions.

In this study, we use empirical data to show the effects of beam trawling disturbance and sediment characteristics and depth on the structure of the infaunal size spectrum in central North Sea fishing grounds. Having demonstrated that trawling disturbance rather than sediment type or depth has the overriding effect on the size structure of the community, we develop a size-based model to examine how spatial and temporal patterns of trawling disturbance affect the production, biomass, and size composition of the infaunal community. The model is parameterized from literature data and by using allometric methods (Yodzis and Innes 1992). We compare model outputs with previously published field data that describe the effects of beam trawling on the production and size composition of benthic communities.

Methods

Effects of trawling disturbance on size structure of the benthic community

We assessed the effects of trawling disturbance and environmental factors on the size structure of the benthic community at seven sites of 1 nautical mile × 1 nautical mile (1 nautical mile = 1.852 km) in the Silver Pit, an important beam trawling ground in the central North Sea. Silver Pit sites generally have fine sediments with high water content and range in depth from 59 to 72 m (Table 1). Silver Pit is more famous as the site of a well-preserved, unique, small crater created by the impact of an extraterrestrial object about 60 million years ago (Stewart and Allen 2002), but the effects of this crater underlying >300 m of tertiary sediment were not considered in our analysis. Further details of the study sites are reported in a companion study (Jennings et al. 2001).

The infaunal invertebrate community at each site was sampled with an anchor dredge during winter and summer. The anchor dredge samples on an appropriate scale for the study of fishing effects (over areas of m^2) and integrates small-scale patchiness of the larger macrofauna (individual body mass >0.0625 g wet weight). Three randomly located replicate tows were completed at each site in each season from the R/V *Corystes*. Winter samples were collected from 22 November to 8 December 1999, and summer samples were collected from 1 to 3 May 2000. A subsample of 0.2 m^3 of sediment was taken from each anchor dredge sample and sieved through 1 mm square mesh. All free-living infaunal species retained by the mesh were removed for processing. All individuals were weighed, either fresh using heave-compensated balances or after preservation in 4% seawater–formalin buffered with 3 $g \cdot L^{-1}$ sodium acetate, and were assigned to $\log_2$ body size categories. Biomass by size class was reported as the mean for the six replicates at each site. Biomass size spectra were normalized by dividing the biomass in a given body mass class interval by the width of that class interval. Trawling disturbance at each site was estimated from records of vessel sightings by fishery-protection aircraft as described by Jennings et al. (2001) and reported as sightings of beam trawlers per unit of searching effort (SPUE) (Table 1). The mean depth at each site was calculated from six measurements taken at random locations during the deployment of the anchor dredge. Five randomly located sediment cores were taken at each site, and one subsample from each core was taken with a 5.5 cm diameter perspex tube inserted to a depth of 10 cm; these samples and overlying water were frozen to –20°C pending analysis. In the laboratory, thawed sediment samples were wet-sieved through a 500-μm sieve, and the fraction greater than 500 μm was oven-dried at 90°C for 24 h. This fraction was then dry-sieved at 0.5-phi intervals, down to 1 phi (500 μm), and weighed on a top pan balance (precision = 0.01 g). The fraction smaller than 500 μm was freeze-dried and analyzed on a Coulter LS 130 laser sizer (Beckman Coulter, Inc., Fullerton, Calif.). The laser sizer results were combined with

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Table 1. Environmental and fishing effort at the Silver Pit study sites.

Site	Water depth (m)	Trawling effort (SPUE × 10^3)	Sediment diameter (mm)	Mean % mud–clay
S1	72±1.2	3.2	0.08±0.015	25
S2	69±1.6	7.9	0.09±0.017	21
S3	67±0.7	14	0.05±0.009	36
S4	65±0.7	12.4	0.06±0.014	25
S5	60±2.9	19.4	0.08±0.025	27
S6	59±0.2	13.7	0.03±0.004	45
S7	60±0.8	0.7	0.02±0.002	34

Note: Depth is the mean depth based on six random measurements during sampling. Beam trawl disturbance is expressed as mean sightings per unit searching effort (SPUE) of beam trawlers by fishery-protection flights. Site codes follow Jennings et al. (2001).

the dry-sieve results to give the full particle size distribution. The mean particle size diameter and sorting coefficient were calculated from these results (Dyer 1986).

Multidimensional scaling (MDS) was used to investigate the biotic relationships between sites. In this analysis, we treated each of the infaunal $\log_2$ body mass classes from –4 to 7 as if it were a species in a conventional community analysis (Schwinghamer 1988) and produced a similarity matrix for the seven sites using a Bray–Curtis similarity measure. The biomass in each of the 12 size classes was $\log_{10}$-normalized biomass (the mean values in the size spectra shown in Jennings et al. 2001).

To examine the relationships between the size structure of the infaunal community, depth, trawling disturbance, and sediment characteristics, we used the BIOENV procedure of Clarke and Ainsworth (1993). This selects the environmental variables best explaining community pattern by maximizing a rank correlation between environmental and community similarity matrices. The environmental similarity matrix was calculated using square root transformed mean depth, trawling disturbance (SPUE), and mean sediment diameter, using a Euclidean distance measure. This community similarity matrix underlies the MDS plot. Mean sediment diameter was used as a surrogate for percent sand and mud–clay when calculating the environmental similarity matrix because there were highly significant correlations between mean sediment diameter and the percentages of sand and mud–clay. All empirical data analyses were conducted using SAS and PRIMER.

Model development

Our model of a soft-sediment benthic community was developed as a difference model in S, version 4, the language used by the program S-Plus 6 (Insightful Corp., Seattle, Wash.). State variables in the model were defined on the basis of body size and three faunal groups: meiofauna (MEIO), soft-bodied macrofauna (SOFT), and hard-bodied macrofauna (HARD). The model contained 37 state variables, five of which were meiofauna, 16 SOFT, and 17 HARD (Table 2). Though there were 37 state variables, they represented only three groups differing in body size. Hence, there were only three sets of parameters and the model is relatively simple in both structure and parameter demands.

Growth of population biomass in each body size – organism type compartment was modeled by modifying the basic Lotka–Volterra competition equations:

$$(1)\qquad \frac{dG_i}{dt} = B_i r_i \left(\frac{C_i - B_i - \alpha_{ij} \dfrac{\sum_j^J B_j}{J}}{C_i} \right)$$

where i and j are competing groups of organisms, G_i is the gross population growth of compartment i, N_i is the number of individuals in the population i, r_i is the specific rate of weight increase of an individual in population i, C_i is the biomass carrying capacity for population i, B is the biomass of a population i or j, α_{ij} is the competitive influence of a unit of the competitor j biomass on the carrying capacity of population i, and J is the number of compartments of competitor j. SOFT and HARD were assumed to be in competition, but MEIO were not assumed to compete with either of the other groups.

The carrying capacity of a compartment was set at a fixed level in all compartments for each of the three faunal groups of organisms. The competitive reduction of carrying capacity of one compartment by biomass in another was done on a group-wide basis. That is, the biomass of HARD negatively affects the carrying capacity of SOFT in the same manner. As a result, the effects of competition are spread over several size classes.

The α_{ij} values for Lotka–Volterra competition are difficult to determine from experimental data as they are products of the model formulation. Accordingly, we derived a value using a prey overlap index for soft- and hard-body benthos from an Ecopath model (Pauly et al. 2000) of the Celtic Sea (J.K. Pinnegar, Centre for Environment, Fisheries and Aquaculture Science, Lowestoft Laboratory, Pakefield Rd., Lowestoft, Suffolk NR33 0HT, United Kingdom, personal communication) in conjunction with specific growth rates as

$$(2)\qquad \alpha_{ij} = O_{ij}\left(1 - \frac{(\bar{r}_j)^\delta}{(\bar{r}_i)^\delta + (\bar{r}_j)^\delta}\right)$$

where α_{ij} is the conversion of a unit of competitor j's biomass from the carrying capacity of competitor i, and O_{ij} is the proportional overlap of shared prey in the diets of competitors i and j, by weight. Food overlap, O_{ij}, is an output of Ecopath models (Pauly et al. 2000) and varies between 0 and 1. $\bar{r}_j$ and $\bar{r}_i$ are the average specific growth rates (eq. 5) of competitors j and i averaged over size classes. In this case i and j are faunal categories (e.g., HARD or SOFT) rather than individual size classes. Competitive difference, δ, either reduces or increases the difference between the values α_{ij} and α_{ji}. Competitive difference, δ, values of <1 decrease the difference ($\alpha_{ij} - \alpha_{ji}$) in the competitive ability of a competitive pair, whereas δ values >1 increase the difference. The same δ value was used for each pair of α determinations.

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Table 2. Model state variables and parameters.

State variable	Shell-free wet weight (mg)	Total wet weight (mg)	Weight class	Carrying capacity (mg sfwwt·m^{-2})	k (year^{-1})	W_∞ (mg sfwwt)	Specific growth rate (year^{-1})	M_{nat}	M_{trl}	O	δ	α
MEIO 1	0.001	0.001	–20	10	4	0.25	26.8	25.03	0.2	—	—	—
MEIO 2	0.005	0.005	–18	10	4	0.25	24.9	23.28	0.2	—	—	—
MEIO 3	0.02	0.02	–16	10	4	0.25	19.0	17.71	0.2	—	—	—
MEIO 4	0.06	0.06	–15	10	4	0.25	9.1	8.57	0.2	—	—	—
MEIO 5	0.2	0.2	–13	10	4	0.25	0.71	0.74	0.2	—	—	—
SOFT 1	1.9	1.9	–10	1200	0.85	700	8.97	8.42	0.2	0.64	0.5	0.23
SOFT 2	5	5	–8	1200	0.85	700	8.76	8.23	0.2	0.64	0.5	0.23
SOFT 3	10	10	–7	1200	0.85	700	8.45	7.94	0.2	0.64	0.5	0.23
SOFT 4	20	20	–6	1200	0.85	700	7.85	7.38	0.2	0.64	0.5	0.23
SOFT 5	40	40	–5	1200	0.85	700	6.77	6.38	0.2	0.64	0.5	0.23
SOFT 6	80	80	–4	1200	0.85	700	5.04	4.77	0.2	0.64	0.5	0.23
SOFT 7	100	100	–4	1200	0.85	700	4.35	4.13	0.2	0.64	0.5	0.23
SOFT 8	125	125	–3	1200	0.85	700	3.62	3.45	0.2	0.64	0.5	0.23
SOFT 9	200	200	–3	1200	0.85	700	2.08	2.02	0.2	0.64	0.5	0.23
SOFT 10	225	225	–3	1200	0.85	700	1.73	1.69	0.2	0.64	0.5	0.23
SOFT 11	300	300	–2	1200	0.85	700	0.99	1	0.2	0.64	0.5	0.23
SOFT 12	350	350	–2	1200	0.85	700	0.69	0.72	0.2	0.64	0.5	0.23
SOFT 13	400	400	–2	1200	0.85	700	0.48	0.53	0.2	0.64	0.5	0.23
SOFT 14	450	450	–2	1200	0.85	700	0.33	0.39	0.2	0.64	0.5	0.23
SOFT 15	475	475	–2	1200	0.85	700	0.27	0.33	0.2	0.64	0.5	0.23
SOFT 16	500	500	–1	1200	0.85	700	0.23	0.3	0.2	0.64	0.5	0.23
HARD 1	50	87.5	–4	6000	0.2	140 000	1.66	1.63	0.26	0.64	0.5	0.41
HARD 2	100	175	–3	6000	0.2	140 000	1.66	1.63	0.26	0.64	0.5	0.41
HARD 3	200	350	–2	6000	0.2	140 000	1.65	1.62	0.26	0.64	0.5	0.41
HARD 4	300	525	–1	6000	0.2	140 000	1.65	1.62	0.27	0.64	0.5	0.41
HARD 5	400	700	–1	6000	0.2	140 000	1.64	1.61	0.27	0.64	0.5	0.41
HARD 6	500	875	–1	6000	0.2	140 000	1.63	1.6	0.27	0.64	0.5	0.41
HARD 7	1000	1750	0	6000	0.2	140 000	1.61	1.58	0.29	0.64	0.5	0.41
HARD 8	3200	5600	2	6000	0.2	140 000	1.49	1.47	0.35	0.64	0.5	0.41
HARD 9	10 000	17 500	4	6000	0.2	140 000	1.18	1.18	0.44	0.64	0.5	0.41
HARD 10	18 500	32 375	5	6000	0.2	140 000	0.88	0.9	0.27	0.64	0.5	0.41
HARD 11	23 000	40 250	5	6000	0.2	140 000	0.76	0.79	0.15	0.64	0.5	0.41
HARD 12	28 000	49 000	5	6000	0.2	140 000	0.64	0.68	0.06	0.64	0.5	0.41
HARD 13	35 000	61 250	5	6000	0.2	140 000	0.50	0.46	0.02	0.64	0.5	0.41
HARD 14	42 000	73 500	6	6000	0.2	140 000	0.40	0.27	0.01	0.64	0.5	0.41
HARD 15	50 000	87 500	6	6000	0.2	140 000	0.30	0.17	0.01	0.64	0.5	0.41
HARD 16	60 000	105 000	6	6000	0.2	140 000	0.21	0.11	0.01	0.64	0.5	0.41

Note: Weight class is $\log_2$ total wet weight (g). Carrying capacity is in shell-free wet weight (sfwwt). Specific growth is calculated from the von Bertalanffy growth curve where the von Bertalanffy growth rate is k (year^{-1}) and the asymptotic weight is W_∞. Natural mortality (M_{nat}) is calculated from specific growth using the relationship from Brey (1999). M_{trl} is the direct mortality rate of fauna resulting from the single passage of a beam trawl. O is the proportional overlap in common diet between the competitive groups SOFT and HARD. The Lotka–Volterra competition coefficient, α, describes the reduction in the carrying capacity of a group by a unit of biomass of the competitor, e.g., a unit of HARD biomass reduces the carry capacity of SOFT by 0.41 units. The exponent in the Lotka–Volterra competition term derivation, which determines the difference in competitive abilities of a competitive pair, is δ.

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If there is no overlap in prey ($O_{ij} = 0$), then i and j do not share any food resources and α_{ij} is 0. This means that i and j do not compete. The limits of α_{ij} as r_j approaches 0 or infinity are O_{ij} or 0, respectively. Therefore a slower-growing prey has a competitive advantage because it reduces the carrying capacity of its competitor. Relatively fast-growing competitors have reduced competitive ability. We consider this a reasonable assumption because slow-growing species often allocate resources to the development of protective structures, whereas fast-growing species often allocate a greater proportion of resources to reproductive output (e.g., Charnov 1993).

The carrying capacity level in the model is simply a scaling factor, i.e., the absolute levels do not affect the model outcomes but the relative difference between size classes and the mechanism itself are important. It must be noted though that the carrying capacity will affect the model dynamics, so greater care needs to be exercised in choosing carrying capacity for a dynamic model. Carrying capacity, C, was chosen as follows:

$$C_{\mathrm{ALL}} = 1$$

$$C_{\mathrm{HARD}} = C_{\mathrm{ALL}}$$

$$C_{\mathrm{SOFT}} = C_{\mathrm{HARD}}/5$$

$$C_{\mathrm{MEIO}} = C_{\mathrm{HARD}}/600 \quad (3)$$

C_{ALL} can then be scaled to reflect the level of biomass in the benthos. The factors for SOFT and MEIO were chosen because they roughly correspond to the relative biomasses of these faunal groups in soft sediment biomass size spectra described in the literature (Schwinghamer 1981; Duplisea 2000) and for the Silver Pit area of the central North Sea (Jennings et al. 2001). All model parameter values are documented here (Table 2) and can be found in the model code (available from first author and for download at http://www.qc.dfo-mpo.gc.ca/iml/en/scientists/DupliseaDE/default.htm).

Growth was modeled using the von Bertalanffy growth equation for weight (Quinn and Deriso 1999):

$$W(t) = W_{\infty}(1 - e^{-kt})^3 \quad (4)$$

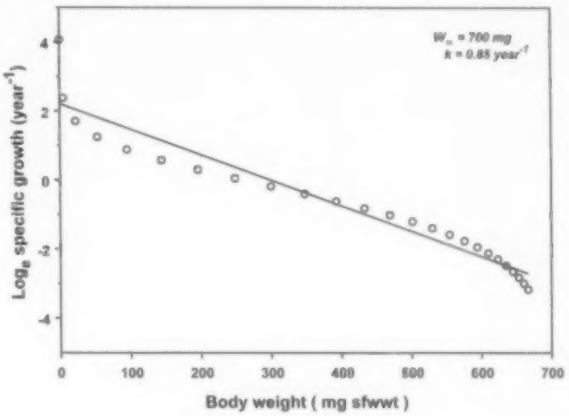
where body weight of an individual, W, is a function of time, t. The Brody growth coefficient is k and W_{∞} is the theoretical asymptotic weight of the individual. Then, by taking the first derivative of eq. 4 and dividing it by the body size at the corresponding time, an expression is obtained for specific growth, r, as a function of time and body weight:

$$r \equiv \frac{\mathrm{d}W/\mathrm{d}t}{W(t)} = \frac{3k_i e^{-kt}}{1 - e^{-kt}} \quad (5)$$

Each of eqs. 4 and 5 was calculated over an appropriate period of time such that the maximum weight was achieved and there was a good range of points at all body sizes to determine a relationship. A log-linear model was then was fitted to these two series, so that we could derive an allometric growth curve for each set of von Bertalanffy growth parameters as

$$\log(r) = aW + b \quad (6)$$

Fig. 1. Specific growth rate of SOFT as a function of soft body size as determined by the von Bertalanffy growth formulation for the SOFT set of parameters. The fitted straight line shown was used to estimate specific growth rate for every body size of SOFT. A similar curve was constructed for each set of growth parameters. Organism shell-free wet weight is abbreviated as sfwwt.



where r is the specific growth rate of an individual, W is the body weight of the individual, and a and b are the fitted coefficients. This fits a linear curve to data that appears as a rotated sigmoidal (Fig. 1). The sigmoidal curve is a function of the von Bertalanffy form of asymptotic growth.

Von Bertalanffy growth rate values (Table 2) were taken from Brey (1999), where SOFT k values are characteristic of organisms such as polychaetes and amphipods and HARD k values are characteristic of those for bivalves and echinoderms. The W_{∞} values were based on the largest organisms recorded in the literature or recorded on surveys conducted in the North Sea by the Centre for Environment, Fisheries and Aquaculture Science (CEFAS) research vessels. Von Bertalanffy growth parameters for meiofauna were not available in the literature and thus von Bertalanffy growth may not be accurate for MEIO; however, in the absence of other information, we continued to use it for the sake of internal consistency.

Instantaneous mortality rates were modeled from specific growth rate using an empirically determined relationship (Brey 1999):

$$M_{\mathrm{nat}} = 0.082 + 0.93r \quad (7)$$

where M_{nat} is the instantaneous natural mortality rate and r is the specific growth rate per year of organisms type size i. Because this relationship primarily applies to small soft-bodied invertebrates, it was modified for the hard organisms by reducing M_{nat} values by factors 1.2, 1.7, 2.1, and 2.6, respectively, for the four largest size classes of hard organisms (Table 2). These values were chosen by "tuning" them so that the modeled production–biomass (P/B) versus body size slope matched empirical curves while keeping a progression of increasing division factors with size.

Mortality resulting from trawling activity was modeled with a continuous formulation:

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$$\text{Mort} = 1 - e^{-(M_{trl}F + M_{nat})} \quad (8)$$

where Mort is the proportion of the population dying per unit time, M_{trl} is the instantaneous mortality rate resulting from trawling activity, and M_{nat} is the instantaneous natural mortality rate. Trawling effort, F, is the number of times per year that an area of the bottom is swept by a trawl.

The mortality rates that result from a single pass of a beam trawl were compiled from Lindeboom and de Groot (1998) and Bergman and van Santbrink (2000*a*, 2000*b*) (Fig. 2; Table 2). We fitted a size-dependent mortality curve to these data to estimate the direct mortality rate on each faunal group and size class. The relationship between HARD mortality was modeled as a Gaussian curve where trawling caused at least 1% mortality and the maximum mortality was 44% (Fig. 2*a*; Table 2):

$$M_{trl(HARD)} = M_{hmin} + (M_{hmin} - M_{hmax})e^{\frac{(W_h - \overline{W_h})^2}{V_h}} \quad (9)$$

where $M_{trl(HARD)}$ is the mortality rate which varies between the minimum mortality rate (M_{hmin}) and maximum mortality rate (M_{hmax}), W_h is the body weight of compartments of h, $\overline{W_h}$ is the mean body weight of HARD, and V_h is the variance of the Gaussian curve describing mortality as a function of size.

The relationship between SOFT and MEIO mortality versus body size was modeled with a simple linear relationship of slope = 0 and intercept halfway between the maximum and minimum observed mortality. The data do not justify the use of a more complex functional form (Fig. 2*b*).

Direct mortality rates (Fig. 2; Table 2), which vary between 0 and 1, were considered to be equivalent to continuous mortality rates for modeling mortality (eq. 8). Continuous mortality usually overestimates survivorship by 2–10% for a trawling mortality rate of 0.2 and up to five trawl passes per year.

Equations 1–9 were combined to give the population biomass flux for a compartment:

$$\frac{dB_i}{dt} = B_i r_i \left(\frac{C_i - B_i - \alpha_{ij} B_j}{C_i} \right) - B_i \text{Mort}_i \quad (10)$$

The model results reported here are for simulations run to steady state with a 30-day time step. Other time steps were used, but because this model is implemented as a difference equation, instabilities arise at large time steps. As time step length decreases, the model makes a better approximation to the continuous formulation used for trawling mortality.

We used the model to simulate the impacts of trawling frequencies ranging from 0 to 10 times per year. This covers the range of trawling frequencies commonly observed on beam trawl fishing grounds in the North Sea (Rijnsdorp et al. 1998; Jennings et al. 1999), although some small patches of ground may be trawled more frequently (Rijnsdorp et al. 1998). Model results are generally presented in the convention of normalized size spectra (Platt and Denman 1977) where biomass in a size category is divided by the width of that category and the result is plotted as $\log_2$ body size versus $\log_2$-normalized biomass.

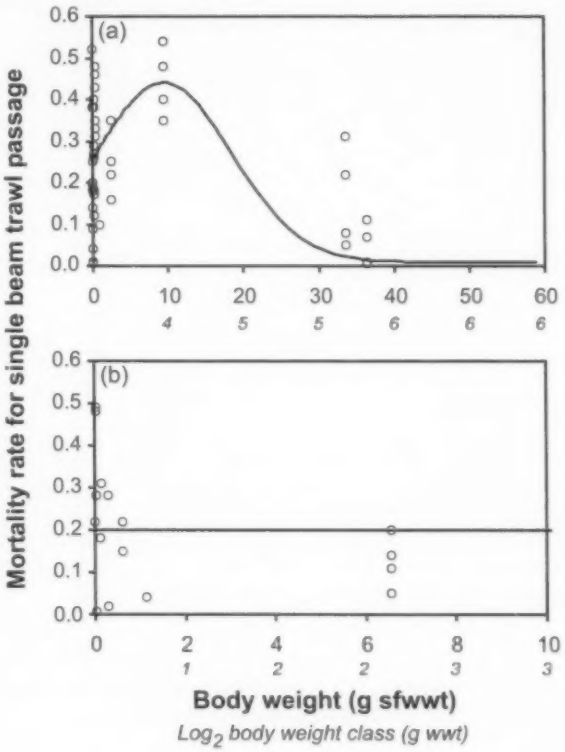

Fig. 2. Direct mortality of (*a*) hard-bodied and (*b*) soft-bodied organisms of different body sizes following a single pass of a 12-m beam trawl. The curves were used to parameterize trawling mortalities for (*a*) HARD and (*b*) SOFT and MEIO. (A secondary *x* axis scaling in body weight class is shown that is consistent with other figures.) Data compiled from Lindeboom and de Groot (1988) and Bergman and van Santbrink (2000*a*, 2000*b*). Organism wet weight is abbreviated as wwt and organism shell-free wet weight as sfwwt.

Results

Effects of trawling disturbance on size structure of the benthic community

Trawling disturbance varied by a factor of 27 among the Silver Pit study sites (Table 1). An MDS plot with trawling disturbance superimposed (Fig. 3) suggested that the size structure of the infaunal communities was largely influenced by trawling disturbance, with sites subject to higher levels of disturbance (S4 and S5) clearly separated from those sites where trawling disturbance was low (S1 and S7). When the BIOENV procedure was used to select the environmental variables best explaining the size structure, the single environmental variable that best grouped the sites in a manner consistent with the size-based community patterns was trawling disturbance (PW = 0.63). No other environmental variable or combination of environmental variables grouped the sites as effectively, the best alternative being the combination of trawling disturbance and mean sediment diameter (PW = 0.62).

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Fig. 3. Multidimensional scaling (MDS) plot as produced by the BIOENV procedure showing the relationship between seven sites in the Silver Pit based on the size structure of the benthic communities. Areas of symbols are proportional to the level of trawling disturbance (see Sightings per unit effort (SPUE), Table 1).

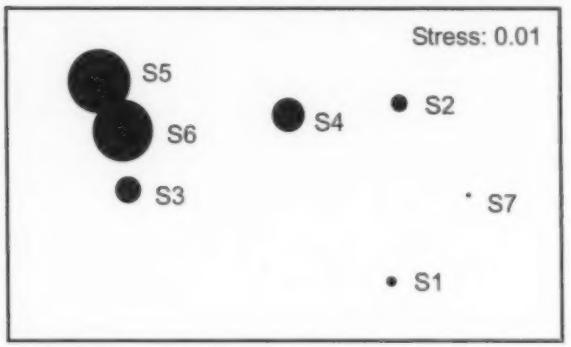
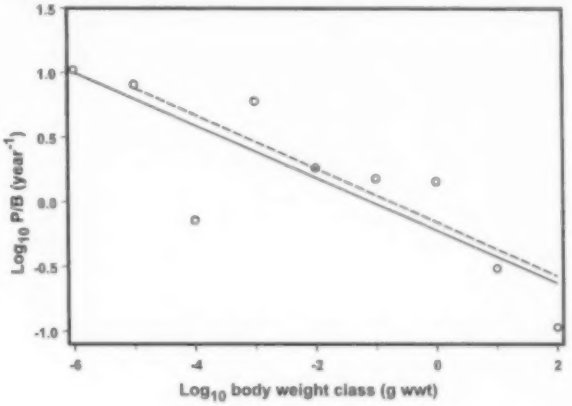


Fig. 4. Production–biomass ratio (*P/B*) versus body size as produced by the present model. For comparison, the empirically determined line for benthic fauna described by Schwinghamer et al. (1986) is depicted as a broken line. The fitted line produced by the model has a slope of –0.20 and intercept of –0.22 year^{-1}. Organism wet weight is abbreviated as wwt.



Model predictions

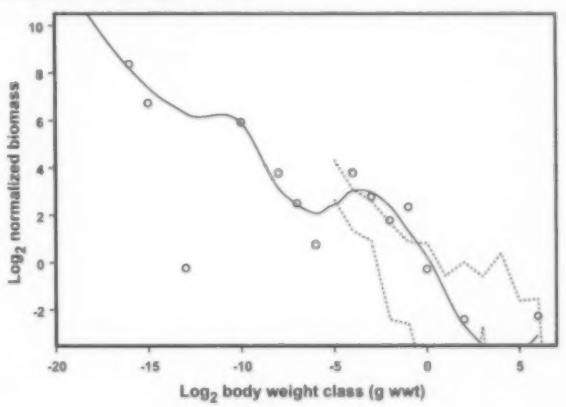
Over all modeled organism size classes, the model generated a *P/B* versus body mass relationship of –0.20 and a within-macrofauna slope of –0.32 (Fig. 4). The modeled normalized biomass size spectrum for a community unaffected by trawling disturbance fell within the range of biomass size spectra determined empirically for sites in the Silver Pit (Fig. 5). The modeled normalized biomass size spectra exhibited a trough in biomass in the size transition between meiofauna and macrofauna and humps in biomass associated with meiofaunal and macrofauna size classes. These spectra corresponded to an increasing interval size spectrum (not normalized spectrum) with maximum biomass occurring at the largest body size (Fig. 5).

The model predicted a reduction in total biomass and in the biomass of larger size classes with trawling (Figs. 6*a*, 6*b*, 7). Size classes >1 g wet weight composed most of the total biomass and were most affected by trawling, whereas the smaller size classes were not so heavily affected by trawling and only accounted for a small proportion of total biomass (Fig. 7). There was a small mortality refuge for the largest size class. This resulted from the modeled low mortality rate for larger animals, which may burrow to greater depths than intermediate-sized individuals. At weight classes near –5 (about 0.03 g wet weight), the biomass of organisms was low in the absence of trawling mortality. As trawling intensity increased, however, their biomass also increased because of a competitive release afforded by the reduction in biomass of their larger competitors (Fig. 6*b*). At the highest trawling intensities, this competitive release was countered by direct mortality, and the biomass maximum moved to an even smaller body size.

For the meiofauna, our model predicted that the largest size classes, with low specific growth rates, would be impacted by relatively low levels of trawling activity. However, the smaller meiofauna, which are very productive and have fast generation times, appear to be relatively unaffected by trawling disturbance (Fig. 6*a*).

Total biomass and biomass of organisms >1 g wet weight decreased by a factor of 3–4 with an increase in trawling frequency from 0 to 10 times per year (Fig. 7). Total production was more sensitive to trawling, showing a decline of more than tenfold over the same trawling frequency range. Largest declines in biomass and production occurred at the initial stages of trawling activity (i.e., at low levels of levels of trawling).

Fig. 5. Modeled biomass size spectrum of benthic organisms in an undisturbed community. The range of empirical data from all sampling stations in the Silver Pit region of the central North Sea is shown as the two broken lines. A spline smoother fitted to the modeled points is shown as the solid line. Organism wet weight is abbreviated as wwt.



A sensitivity analysis of selected model parameters indicated that von Bertalanffy growth rates were usually most important in determining modeled steady state biomass in SOFT and HARD. Furthermore, their importance increased with trawling frequency. As might be expected, the direct trawling mortality estimates were very important in determining community response to trawling activity. A detailed

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Fig. 6. Normalized biomass size spectra of a simulated steady state community at different levels of simulated trawling intensity. (*a*) The entire spectrum over a trawling intensity range of 0–15 times per year. (*b*) The same spectrum as in (*a*) in greater detail for larger size classes in the trawling range of 0–1 times per year. Organism wet weight is abbreviated as wwt.

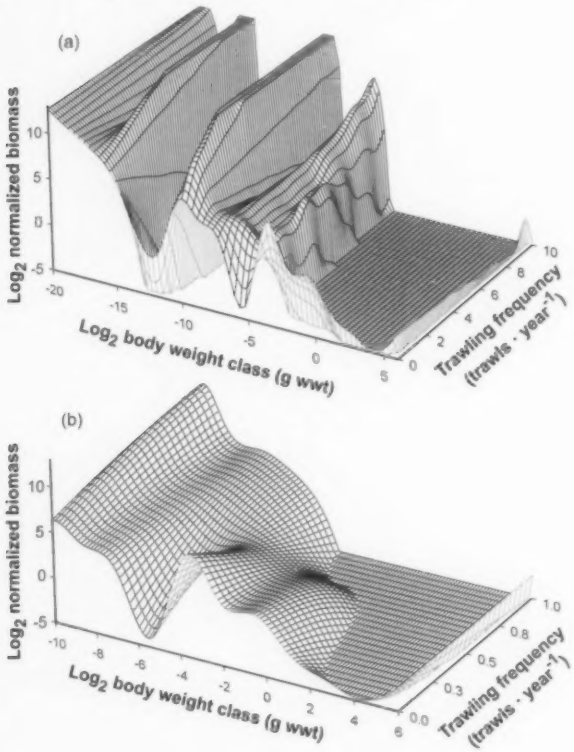
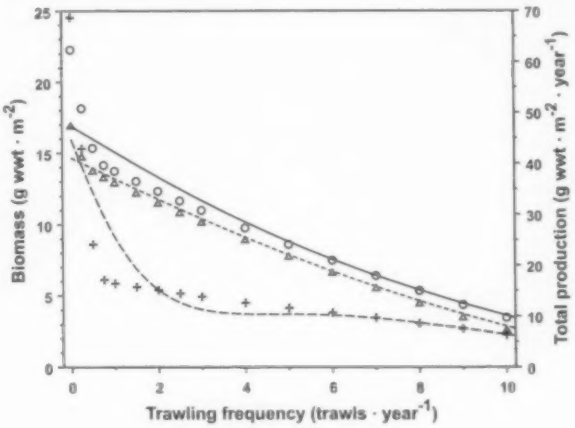


Fig. 7. Total biomass and biomass in size classes >1 g wet weight (wwt) of the modeled benthic community versus trawling intensity: solid line and circles, total biomass; short-dashed line and triangles, biomass in organism sizes >1 g wet weight (wwt); and long-dashed line and crosses, production. Lines represent spline smoothers through the modeled data points.



sensitivity analysis is available from the author and at http://www.qc.dfo-mpo.gc.ca/iml/en/scientists/DupliseaDE/default.htm.

Discussion

Trawling disturbance, as opposed to measured environmental factors, had an overriding effect on the size structure of the benthic infaunal community in the Silver Pit. This size-based response provided a compelling reason to develop a size-based model of the effects of trawling disturbance on benthic community structure. The resultant model was internally consistent and generated *P*/*B* versus body mass relationships consistent with those reported in empirical studies (Schwinghamer et al. 1986; Dickie et al. 1987), and the modeled size spectra, total biomass, and total production have empirical support from the companion study to the present work (Jennings et al. 2001).

The model showed a clear decline in total community biomass, biomass of larger macrofauna, and a total production with increases in trawling frequency and sustained trawling activity. That is, there is initially a large decline in the community *P*/*B* followed by a gradual increase. This is consistent with small, fast-growing fauna with low biomass contributing relatively more to community production with trawling frequency. This is corroborated by the decline of large fauna in the biomass spectrum with increased trawling frequency. Change of specific production or respiration is a phenomenon known to occur in disturbed communities where the community is dependent on more resilient smaller fauna (Duplisea and Hargrave 1996). These fauna are often not the macrofauna used by fish as food; hence, it is unlikely that their production would be transferred to the fisheries-related food web.

Our model is applicable to the trawling impacted infaunal communities of mobile sand–mud sediments in the central North Sea. Any application of the model to other locations would require new empirical estimates of mortality functions because mortality rates are strongly dependent on the size-related distribution of animals in the sediment and the penetration depth of the fishing gear (Lindeboom and de Groot 1998). The model outputs implied that the biomass of the larger fauna is reduced by trawling disturbance, consistent with the results of empirical studies in the central North Sea (Jennings et al. 2001). However, the model suggested that this reduction in biomass was not a direct function of body size at all trawling intensities because some of the largest animals suffered lower trawling mortality than intermediate-sized animals (Bergman and van Santbrink 2000*a*, 2000*b*). At moderate trawling intensity, for example, the model suggested that the biomass of intermediate-sized fauna was reduced in relation to that of the largest animals because the largest animals suffered lower mortality than moderate-sized animals that lived closer to the surface of the sediment (Bergman and van Santbrink 2000*a*, 2000*b*). However, at higher trawling intensities, the relatively low population growth rates of the largest animals were not high enough to sustain any elevated mortality resulting from trawling, and their biomass de-

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creased in relation to that of intermediate-sized animals with higher population growth rates. Because the size – trawling mortality relationship is a key component of this model, further empirical work should aim at its amelioration.

We made a number of simplifying assumptions when formulating the model, and although the model is implemented in a dynamic form, it is presently valid only at steady state. We modeled the population growth of three types of organisms in several size classes, but there is no growth between size classes to link the growth of individuals through the size spectrum. Therefore, the abundance of large HARD, for example, is not directly related to the abundance of small HARD. Moreover, we ignored the processes that link the reproductive output of mature individuals to the recruitment of juveniles, which is very poorly known at present. Both these factors could be incorporated in subsequent developments of the model and would be needed for its application in system-wide management of trawl fishery impacts.

The asymptotic growth formulation that we used means that an organism approaching its maximum size will have a growth rate tending to zero. Therefore, in some parts of the size spectrum, there is low biomass because there is only a very low population growth rate of organisms there. This is both real because biomass troughs are observed in benthic and pelagic size spectra (Schwinghamer 1981; Sprules and Goyke 1994) and an artefact arising from only three different growth trajectories being used rather than the continuum that would be present in a multispecies community. In the present model, the location of near-zero biomass values corresponded with those observed in real spectra (e.g., Schwinghamer 1981), but it is important not to overinterpret bumps in the size spectrum of individual organism types.

We assumed that mortality could be estimated from specific growth using a published empirical relationship (eq. 6). This relationship was interpolated between the sizes of MEIO 5, SOFT 11–15, and HARD 10–12, but we had to extrapolate it to other size categories. As a result, predicted mortality rates may be too high or low for some categories; however, when trawling mortality contributes a large proportion of total mortality, errors in modeling natural mortality are less important. Further improvements to the model should account for mortality in a more mechanistic manner that models mortality rates for all size categories.

At the lowest trawling intensities, the model predicted that there was a "dip" in the biomass of small macrofauna, but this dip was lost at higher trawling intensities. This is a result of competition, where the high biomass of large fauna at low trawling intensities reduces the biomass of smaller fauna. As trawling intensity increases, the biomass of larger macrofauna is reduced and the smaller macrofauna can compete more effectively. These outputs suggest that the processes structuring trawled and untrawled benthic communities will be very different, with untrawled communities in areas of low natural disturbance dominated by larger macrofauna that limit the growth of smaller individuals. For meiofauna, our model predicted that the largest size classes, with low specific growth rates, would be impacted by relatively low levels of trawling activity. However, the smaller meiofauna that are very productive and have fast generation times appear to be relatively unaffected by trawling disturbance. Unfortunately, at present, there are few empirical data to determine whether the predicted changes in MEIO resulting from trawling are consistent with those that actually occur in meiobenthic communities (Schratzberger et al. 2002).

Clearly, the current model would need further modification and testing before the outputs are used for quantitative prediction and to support management advice. The size-based approach to modeling trawling impacts, however, should be recognized for its many useful properties such as simple structure, low parameter demands, and general applicability to entire communities rather than specific taxa. Moreover, because so many characteristics of organism metabolism, community structure, and trawl-induced organism mortality are size-based, the present model structure provides a useful and biologically grounded description of the community and its response to trawling.

Both the model and existing empirical studies suggest that North Sea populations of intermediate- and large-sized macrofauna cannot tolerate moderate (~2 passes·year^{-1}) levels of trawling disturbance (Piet et al. 2000; Rumohr and Kujawski 2000; Jennings et al. 2001). However, there is little evidence for the extirpation of intermediate- and large- sized macrofauna over the whole of the central North Sea, even though their abundance is much reduced. We suggest that their persistence is a consequence of the patchiness of trawling disturbance at many scales, with some areas of the seabed trawled five or more times per year while others are virtually untrawled. If the same trawling effort were distributed homogeneously, it is unlikely that populations of these animals would persist. In the North Sea, the significance of patchiness in trawling disturbance is likely to be considerable. At the scale of the ICES (International Council for the Exploration of the Sea) rectangle (211 rectangles of 0.5° latitude by 1° longitude: area of rectangle 3720 km^2 at 53°N), 50% of rectangles are beam-trawled for less than 2000 h·year^{-1} (Jennings et al. 1999). Because a typical beam trawler tows two 12 m wide beams at 6 knots (11 km·h^{-1}), it will impact 534.5 km^2 of the seabed in 2000 h. Thus, in rectangles subject to 2000 h beam trawling·year^{-1} and with a truly homogeneous effort distribution in the rectangle, it would take at least 7 years to trawl the entire rectangle once. Both our model and empirical studies suggest that this frequency of trawling (0.14 times·year^{-1}) would have a relatively minor effect on the benthic infaunal community in sandy sediments.

At the North Sea scale, of course, the distribution of trawling effort among rectangles reflects the presence of sand and sand–mud habitats that can be beam-trawled, so not all lightly trawled rectangles may support comparable populations of intermediate- and large-sized macroinfauna. When distributions of trawling disturbance are examined at even finer scales on comparable habitats, the patchiness in disturbance is still apparent. Rijnsdorp et al. (1998), for example, looked at the patchiness of beam trawling effort on the fishing grounds used by the Dutch fleet in the southern and central North Sea. The degree of patchiness decreased as the resolution of their analyses was increased from 30 × 30, to 10 × 10, to 3 × 3, to 1 × 1 nautical miles. In 1 × 1 nautical mile boxes, the distribution of effort was considered random in 90% of cases. In eight of the most heavily trawled ICES

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rectangles in the southern North Sea (total area 7200 nautical mile^2), 5% of the area was trawled less than once in 5 years and 70% was trawled more than once per year. Because trawling frequencies of greater than once per year would exterminate some of the intermediate-sized macrofauna, we can only assume that their persistence in parts of the North Sea is due to their presence in occasionally trawled areas and habitats unsuitable for trawling, both of which can also act as sources of recruitment.

It is also important for the persistence of intermediate-sized macrofauna that similar patterns of spatial heterogeneity in trawling effort are maintained from year to year. Over the 4 years of the Rijnsdorp et al. (1998) study, this appeared to be the case. In the absence of changes to management strategies that result in the relocation of effort, some consistency in spatial effort distribution is expected from year to year because trawlers will tend to return to tows that are stored on their navigation systems and known to be clear of obstructions. We suggest that management measures that reduce patchiness in trawling disturbance or affect the persistence of spatial patterns in effort over time are likely to have greater effects on benthic communities than those that encourage small areas to be fished repeatedly.

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Interactive effects of temperature and salinity on otolith chemistry: challenges for determining environmental histories of fish

Travis S. Elsdon and Bronwyn M. Gillanders

Abstract: The concentrations of elements and isotopes in fish otoliths may provide a method of reconstructing movements of fish by differentiating between water bodies of different temperatures and salinities. However, before otoliths can be used to reconstruct environmental histories of fish, it is necessary to assess the effects of seawater temperature and salinity on otolith microchemistry. Using controlled laboratory experiments, juvenile black bream, *Acanthopagrus butcheri* (family Sparidae), were reared for 50 days in aquaria of varying temperatures and salinities using three experimental designs: temperature × salinity, temperature only, and salinity only. Temperature and salinity interacted to significantly affect the elemental concentration ratios of Sr:Ca and Ba:Ca and the concentrations of isotopes $\delta^{13}C$ and $\delta^{18}O$ in otoliths. The single-factor experiments showed that temperature significantly affected the concentration ratios of Sr:Ca and Ba:Ca and the concentrations of $\delta^{13}C$ and $\delta^{18}O$ in otoliths, whereas salinity alone did not affect the concentration ratios of any elements but did affect both isotopes. The concentration ratios of Mg:Ca and Mn:Ca varied considerably among fish within the same treatment level and showed little or no effects due to temperature and (or) salinity. The significant interactive effects of temperature and salinity on otolith microchemistry highlight the need for a multifactorial approach to testing hypotheses regarding the environmental histories of fish.

Résumé : Les concentrations d'éléments et d'isotopes dans les otolithes de poissons peuvent fournir une méthode pour retracer les déplacements des poissons en discriminant entre des masses d'eau de températures et de salinités différentes. Cependant, avant que les otolithes ne puissent servir à récapituler l'histoire environnementale des poissons, il est nécessaire de déterminer les effets de la température et de la salinité de l'eau de mer sur la microchimie des otolithes. Dans des expériences de laboratoire contrôlées, nous avons élevé des jeunes « brèmes noires », *Acanthopagrus butcheri* (famille des Sparidae), durant 50 jours dans des aquariums de salinités et de températures différentes selon trois plans d'expérience: température × salinité, température seule et salinité seule. La température et la salinité interagissent pour affecter de façon significative les rapports des concentrations d'éléments Sr:Ca et Ba:Ca,, ainsi que des isotopes $\delta^{13}C$ et $\delta^{18}O$ dans les otolithes. Les expériences qui tiennent compte des facteurs séparément indiquent que la température affecte de façon significative les rapports des concentrations de Sr:Ca, Ba:Ca, $\delta^{13}C$ et $\delta^{18}O$ dans les otolithes, alors que la salinité seule n'affecte pas les rapports des éléments, mais seulement les deux isotopes. Les rapports des concentrations de Mg:Ca varient considérablement chez les poissons soumis à un même traitement et ne sont que peu affectés par la température et/ou par la salinité ou alors ne sont pas affectés du tout. Les effets significatifs de l'interaction de la température et de la salinité dans la microchimie des otolithes mettent en relief la nécessité d'adopter une approche multifactorielle dans l'évaluation des hypothèses sur l'histoire environnementale des poissons.

[Traduit par la Rédaction]

Introduction

One of the most recent developments in fisheries science is the use of elemental and isotopic concentrations of calcified structures as chemical fingerprints or natural tags. These chemical fingerprints can potentially be used to discriminate between fish that have inhabited different water bodies (e.g., discriminate between nursery areas (Gillanders and Kingsford 2000) and different stocks (Edmonds et al. 1999)) and can therefore determine migration patterns of individuals and, more broadly, define fish stocks. The most widely used calcified structure for stock discrimination and movement studies are otoliths, which are suspended in endolymph fluid within the inner ear (Campana 1999). Formation of new otolith material occurs when calcium carbonate ($CaCO_3$) crystallizes out of the endolymph fluid onto the outer surface of the otolith, with this growth corresponding to daily, seasonal, and annual increments (Campana and Neilson 1985). As calcium carbonate crystallizes onto the otolith surface, elements such as carbon (C), oxygen (O), calcium (Ca), strontium (Sr), magnesium (Mg), manganese (Mn), and barium (Ba) along with other elements are incorporated into the

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carbonate matrix. Elements in the water pass through three main interfaces (brachial uptake, cellular transport, and crystallization) before they are incorporated into the otolith. The presence of these interfaces, which may concentrate or dilute elements and isotopes, ensures that otoliths, unlike other calcified structures (e.g., bivalve shells (Campana and Thorrold 2001)), do not necessarily directly reflect the elemental or isotopic composition of the surrounding seawater. Thus, the assimilation of elements and isotopes into otoliths is likely to be influenced by both physiological processes (Kalish 1989; Hoff and Fuiman 1993; Campana 1999) and environmental variables such as temperature and salinity (Fowler et al. 1995*a*; Hoff and Fuiman 1995; Thorrold et al. 1997).

Temperature and salinity do not vary independently of one another in seawater and can vary over small spatial scales, both vertically in the water column and horizontally between different water bodies (e.g., Bisagni et al. 2001). Temperature and salinity can also influence elemental and isotopic concentrations in seawater (e.g., Epstein and Mayeda 1953). As fish migrate they may inhabit waters of varying temperature and salinity. Hence, determining the effects of temperature and salinity on the incorporation of elements and isotopes into otoliths enhances our ability to interpret movement and migration patterns (e.g., Milton et al. 2000), stock structure of fish (Edmonds et al. 1999; Campana et al. 2000), and temperature and salinity histories of fish (e.g., Patterson 1999) based on otolith microchemistry.

The influence of temperature and salinity on the concentration of elements in otoliths has largely been determined by field studies where fish collected from environments with different temperature and salinity regimes (e.g., freshwater, estuarine, and marine waters, see Tzeng et al. 1997) are compared. Such studies assume that the otolith area was deposited while the fish inhabited a particular body of water; however, temperature and (or) salinity at the time of otolith deposition is often unknown. There have been several controlled experimental evaluations reporting varied results on the effects of temperature alone (e.g., Tzeng 1996; Chesney et al. 1998; Kawakami et al. 1998) and salinity alone (e.g., Hoff and Fuiman 1995; Secor et al. 1995; Tzeng 1996) on the concentration of elements in otoliths. Most of these experiments have focused on microelements (e.g., Na, Mg, Sr), and there have been relatively few experiments examining trace elements (e.g., Ba and Mn, but see Fowler et al. 1995*a* and 1995*b* and Hoff and Fuiman 1995). There have been fewer experiments successfully rearing fish under orthogonal combinations of temperature and salinity (Secor et al. 1995; Tzeng 1996; Chesney et al. 1998).

Much of the research on the influence of temperature and salinity on carbon and oxygen isotopes has been inferred through correlative studies (e.g., Patterson 1999). Although there are several examples of isotopes being used to discriminate between fish inhabiting different water masses (e.g., Edmonds et al. 1999), the environmental factors that cause these differences in otolith isotopic concentration remain largely unknown. Several experiments have assessed the effect of temperature on otolith oxygen and carbon isotopic concentrations (Kalish 1991*a*; Radtke et al. 1996; Thorrold et al. 1997). All experiments found a positive relationship between oxygen isotopic concentrations and temperature, whereas carbon isotopic results displayed both negative and nonsignificant trends with temperature. The influence of salinity on stable isotope concentrations of otoliths remains untested, and similarly, there have been no orthogonally designed experiments examining the effects of temperature and salinity on isotope concentrations.

The lack of experimental evidence describing the relative and interactive effects of temperature and salinity on otolith elemental and isotopic concentrations represents a significant void in otolith research and is a severe inhibitor to our understanding of the role that otolith microchemistry can play in determining migratory patterns of fish. The objective of this study was to determine if otolith microchemistry of black bream (*Acanthopagrus butcheri*, family Sparidae), a commercially important species that occupies a wide range of temperatures and salinities, is influenced by seawater temperature and salinity. Specifically, controlled laboratory experiments that manipulated temperature and salinity and an orthogonal combination of both factors were used to determine the relative and interactive effects of these parameters on the elemental and isotopic concentrations of bream otoliths.

Materials and methods

Experimental design

Juvenile black bream (*A. butcheri*) ~20 mm in total length were obtained from a local hatchery (Clean Seas Aquaculture, Arno Bay, South Australia) and held in a 300-L fibreglass tank equipped with adequate air and water filtration. The fish were bred from a common brood stock, thus reducing genetic variability. Fish were allowed to acclimatize for 2 days under similar conditions to those in which they were reared (22°C and 30‰), after which they were subjected to experimental treatments. All seawater used during the rearing process was collected weekly from the South Australian Research and Development Institute (SARDI) Aquatic Sciences facility and was held in a 2000-L indoor aerated tank, which was covered to reduce evaporation. Fish were fed a mixed diet of commercial bream food, flake food, live brine shrimp (*Artemia* sp.), and black worms (*Tubifex* sp.) throughout the duration of the experiment. Light was provided from fluorescent tubes on a 12-h day – 12-h night cycle in a constant-temperature room.

Otoliths were marked at the end of the acclimatization period by immersing fish in a tetracycline hydrochloride bath (250 $mg \cdot L^{-1}$) for 16 h (e.g., Kalish 1989). This enabled the differentiation of old otolith growth (at the hatchery) from new otolith growth (under experimental conditions). Immediately after the tetracycline bath, fish were randomly assigned to experimental treatments at densities of 11–13 fish per tank. Each experimental tank consisted of a 40-L high density polyethylene tub (sterilized using bleach) with adequate aeration and a clear plexiglass cover to minimize evaporation (and hence salinity changes).

Three experiments were set up: (1) temperature × salinity manipulations arranged in an orthogonal two-way design to test the relative and interactive effect of these two factors, (2) temperature manipulations in a one-way design to test the effect of a broad range of temperatures (12, 16, 20, 24, 28°C) at a constant salinity (30‰), and (3) salinity manipulations in a one-way design to test the effect of a broad range of salinities (5, 11, 17, 23, 30‰) at a constant temper-

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ature (16°C). Treatments in the orthogonal two-way experiment of temperature × salinity consisted of all possible combinations of three temperatures (16, 20, and 24°C) and three salinities (5, 17, and 30‰). For all experiments, each treatment level had duplicate tanks.

The experimental conditions in each tank containing fish were established by adjusting the temperature and salinity of the water at a rate of 2°C per day and 3.5‰ per day until the desired temperatures and (or) salinities were obtained. Temperature conditions were maintained using chiller units (12°C tanks) and aquarium heaters (20°C and higher temperature tanks). The desired salinity for each treatment was established by mixing seawater with deionized water to the desired concentration. One-quarter of the water in each tank was changed every 2nd day, at which time any accumulated detritus was siphoned away. During the rearing period, temperature and salinity were monitored daily.

After 50 days of exposure to the experimental conditions, all fish were immersed in an ice slurry. For each fish, the standard length was measured and the sagittal otoliths were dissected, washed and cleaned in deionized (Milli-Q, Millipore) water, and allowed to dry before being stored in microcentrifuge tubes. One otolith from each pair was weighed using an electrobalance (accuracy to 0.00001 g). The otoliths of seven fish from each tank (the maximum number available at the end of the experiment for a balanced design) were then chosen for analysis of elemental and isotopic concentrations based on the similarities of otolith weights because otolith weight is likely to influence otolith chemistry. Previous work has found that the analysis of seven fish is adequate given the low variability of otolith chemistry among replicates (Dove et al. 1996).

General sample preparation

All sample cleaning and diluting was done using deionized water, as was the cleaning of all materials. Plasticware and glassware were soaked in 10% HNO_3 for at least 24 h and rinsed several times in deionized water before use. The final preparation of samples was done in a plastic laminar flow cabinet to reduce possible airborne sources of contamination.

Elements in otoliths

An otolith from each fish was embedded in Epofix resin (Struers), sectioned transversely through the focus (centre section) to a thickness of approximately 300 μm using a low-speed diamond saw, and polished using 9-μm aluminium oxide lapping film to approximately 200-μm thickness. Polished sections were cleaned in deionized water and dried on glass, after which they were sonicated (cleaned) for 5 min and allowed to dry overnight in a laminar flow cabinet before being mounted on microscope slides. These mounted slides were again dried in a laminar flow cabinet overnight and stored in clean plastic sealable bags awaiting analysis.

The outside edges of otoliths from *A. butcheri* were sampled to ensure that the ablated material was laid down under experimental conditions. This was confirmed by prior examination of the position of the tetracycline fluorescent band. The concentration of elements (Sr, Mn, Ba, Mg, Ca) in the otolith sample was determined using a Merchantek LUV 266 Q-switched Nd:YAG UV laser microprobe (New Wave Research), with a pulse rate of 6.00 Hz and ablation spot size of 100 μm. The laser was connected to a Finnigan MAT ELEMENT HR–ICP–MS (high resolution – inductively coupled plasma – mass spectrometer; Thermo-Finnigan) with gas-flow parameters of coolant 14.00, axillary 1.55, sample 1.5, and helium 0.36 $L \cdot min^{-1}$. Ablation of the otolith material occurred inside a sealed chamber. The ablated sample was extracted from the chamber and transported to the ICP–MS, via a settlement chamber, by an argon and helium gas stream. The ablation chamber was purged for 20 s after each opening to remove any background gas or sample particle that may have contaminated further samplings (see Lahaye et al. 1997 for a detailed description of the machine setup).

Blank ablations, which consisted of measuring the sample gases without ablation, were analyzed before and after each sampling session (for approximately 120 s) to determine detection limits. A reference standard (National Institute of Standards and Technology, NIST 612) was measured after every 12 ablations to correct for low-frequency drift resulting from changes in room temperature, plasma, and electronics (Ludden et al. 1995). The analytical accuracy for the NIST standard averaged across all samples was 100% recovery for all elements; results were reproducible to within 0.0015 (Mg), 0.0003 (Mn), 0.0004 (Sr), and 0.0001 $\mu mol \cdot mol^{-1}$ (Ba). Calcium was used as an internal standard, and therefore, the actual Ca concentrations in the otoliths of each treatment level were determined using AAS (atomic absorption spectrometry); reproducibility was 1%. Samples for Ca analysis (200–600 μg) were obtained by chipping the edge of otoliths from each treatment group (described in isotopes of otolith section in the methods). Chips were diluted in 4 mL concentrated nitric acid and further diluted to 20 mL with deionized water before analysis. The concentrations of each element (Mg, Mn, Sr, Ba) were standardized to calcium by expressing as a ratio to Ca, thus giving values in concentration ratios.

Elements in water

During the rearing period, three 50-mL water samples were collected from each treatment tank, 25 mL of which was filtered through a 0.45 μm filter and acidified with 500 μL of high-grade nitric acid. Samples were refrigerated until further diluted (1:10, sample–deionized water) prior to analysis.

Water samples were analyzed using a DV ICP–AES (dual-view inductively coupled plasma – atomic emission spectrometer; Perkin-Elmer) for the analysis of Ca and Mg and a DRC ICP–MS (dynamic reaction cell inductively coupled plasma – mass spectrometer; Perkin-Elmer) for the analysis of Mn, Sr, and Ba. During the analysis, blanks (prepared in the same manner as samples but with deionized water instead of seawater), spiked blanks (elements spiked into blank sample in known quantities), and standard solutions were analyzed every 10–15 samples and used to correct for background concentrations, assess accuracy and precision of sampling and calculate concentrations in samples. Internal standards of indium (In; 5 ppb) and lutetium (Lu; 2 ppm) were used to correct for drift of ICP–MS and ICP–AES instruments, respectively. The analytical accuracy of elements averaged across all samples was 91 (Ca), 96 (Mg), 110 (Mn), 82 (Sr), and 92% (Ba), with reproducibility of <0.0001 (Ca, Mg, Sr, Ba) and 0.0036 $\mu mol \cdot mol^{-1}$ (Mn). The concentration of each element (Mg, Mn, Sr, Ba) was stan-

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dardized by expressing as a ratio to calcium as these elements are likely to substitute for calcium in otoliths (Campana 1999) and the incorporation of these elements are dependent on the calcium in the water and not the absolute concentrations of the elements.

Isotopes in otoliths

Chips from the outside edges of the dorsal and ventral ends of the second otolith of each fish were collected for isotope analysis. Under a dissecting microscope, whole otoliths were imbedded in adhesive, and based on the position of the fluorescent band, a clean scalpel was used to remove chips from the outside edge so that the chips represented experimental otolith growth. Otolith chips (approximately 250 µg) were placed in a microcentrifuge tube with a 5% H_2O_2 solution and sonicated for 1 h to remove organic material. Cleaned otolith chips were washed several times with deionized water and allowed to dry overnight inside a laminar flow cabinet, after which they were stored in screw-cap plastic vials awaiting analysis.

The concentrations of carbon and oxygen isotopes in the otolith chips were determined using a Finnigan MAT 261 mass spectrometer. Blank samples, NIST standards, and bicarbonate standards were used to assess possible instrument drift. Results were reproducible to within 0.1‰ for both $\delta^{13}C$ and $\delta^{18}O$. Carbon isotope concentrations were standardized to PDB (Peedee belemnite; Epstein and Mayeda 1953) and oxygen isotope concentrations were standardized to SMOW (standard mean ocean water; Coplen 1988), both expressed as parts per thousand (‰).

Isotopes in water

During the rearing process, three water samples were collected in high density polyethylene bottles and were frozen immediately on return to the laboratory. Water samples were prepared for carbon isotope analysis by acidification with H_3PO_4 under a vacuum, followed by cryogenic purification of the gas. Water samples were prepared for oxygen isotope analysis via equilibration with CO_2 at 25°C for 24 h (Kroopnick 1974). The extracted gases for carbon and oxygen isotopes were analyzed using a Finnigan MAT 252 mass spectrometer, and standard solutions were used to assess instrumental drift. Results were reproducible to within 0.2‰ for both $\delta^{13}C$ and $\delta^{18}O$. Carbon isotope concentrations were standardized to PDB and oxygen isotope concentrations were standardized to SMOW.

Statistical analyses

Univariate statistical techniques were used to test hypotheses relating to differences in temperature and salinity of the rearing conditions, as well as differences in fish otolith weight between treatment groups. Univariate statistical techniques were also used to test hypotheses relating to individual elemental concentration ratios (Mg:Ca, Mn:Ca, Sr:Ca, and Ba:Ca) and concentrations of isotopes ($\delta^{13}C$ and $\delta^{18}O$) of *A. butcheri* reared under different treatment conditions. To compare the elements and isotopes among treatments in each experiment (temperature × salinity, temperature, and salinity), analyses of variance (ANOVA) were used. Temperature and salinity were treated as fixed factors and tank, a random factor, was nested within treatments. If variances were heterogeneous (Cochran's C test, $P < 0.05$), data were $\ln(X + 1)$ transformed, after which homogeneity of variance was always obtained. Where significant effects of treatments were detected (i.e., $P < 0.05$), means were compared using Student–Newman–Keuls (SNK) multiple-comparison tests. Backwards stepwise regression analyses were used to determine which of the variables (temperature–salinity treatment, ambient water chemistry, and otolith weight) significantly influenced the concentration of the element or isotope in the otolith. The regression analyses assume a linear relationship between the variable of interest and the concentrations in the otolith, an assumption that may not have always been met by the data.

Multivariate analysis was done for each experiment using a nonparametric multivariate analysis of variance, NP-MANOVA (Anderson 2001). The test statistic is an F ratio similar to that of ANOVA calculated using sum of squares. To test the null hypothesis of no-treatment effect, data were permuted by shuffling the means of each factor level into different levels for the one-way experiment, and for the two-way analysis, the means for a particular level of factor 1 and a particular level of factor 2 were permuted by shuffling these into different levels (Anderson 2001). Temperature and salinity were treated as fixed factors (all tests) for the two-way experiments and tank-nested within treatments for the one-way experiments of temperature and salinity. Euclidean distances were used as the data correspond to environmental variables (Legendre and Legendre 1998). Data were $\ln(X + 1)$ transformed as some elemental ratios and isotopes were in large concentrations relative to others. Temperature × salinity tests used permutations of residuals under a reduced model, whereas temperature-only and salinity-only tests used permutations of residuals under a full model. The number of permutations for all tests was 4999. Where significant differences were detected (i.e., $P < 0.05$), multiple pairwise comparison testing for differences among treatments were performed, with a significance level for each pairwise test of $\alpha = 0.05$. There was no correction to significance levels for the multiple tests, although it would be expected that one in 20 tests would be significant by chance alone.

Nonmetric multidimensional scaling (MDS) was used to visually represent the data. The dissimilarity matrix was calculated using Euclidean distances. Centroids of each treatment group (e.g., centroids of tanks in the salinity experiment) were plotted and stress coefficients were determined, where a stress value of less than 0.2 is acceptable and stress close to 0 indicates that the data are perfectly represented (Clarke 1993). The final MDS plots are only determined to within an arbitrary orientation, reflection, location, and scale, which explains the absence of axes scales and labels in the figures (Clarke 1993).

Results

Rearing conditions and fish growth

Temperature and salinity regimes within the treatment tanks for each experiment did not overlap throughout the duration of all experiments. Furthermore, little variation was detected in the rearing conditions of temperature and salinity between replicate tanks (Table 1). Although the elemental ratio and isotopic concentrations in the rearing water were not manip-

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Table 1. Summary of the rearing conditions within treatment tanks for the three experiments.

Treatment	Tank	Temperature, °C (n = 50)	Salinity, ‰ (n = 50)	SL, mm (n = 7)	Otolith weight, mg (n = 7)
12°C, 30‰ #	1	12.81±0.11	30.24±0.16	36.10±0.56	1.02±0.02
	2	13.06±0.07	29.81±0.17	36.54±0.58	1.03±0.06
16°C, 30‰ #*†	1	15.86±0.14	30.48±0.18	38.97±0.95	1.20±0.06
	2	15.95±0.18	30.21±0.16	40.86±0.83	1.32±0.06
20°C, 30‰ #*	1	20.23±0.10	30.00±0.16	45.80±0.72	1.70±0.02
	2	20.16±0.10	29.68±0.20	43.38±0.97	1.68±0.08
24°C, 30‰ #*	1	24.12±0.10	30.27±0.20	52.03±1.09	2.58±0.10
	2	23.85±0.12	30.33±0.18	52.42±1.35	2.51±0.12
28°C, 30‰ #	1	27.93±0.09	30.38±0.20	56.01±1.85	2.94±0.24
	2	27.70±0.08	30.48±0.15	59.67±1.68	3.17±0.22
16°C, 23‰ †	1	15.44±0.01	23.06±0.05	41.84±1.19	1.46±0.10
	2	15.42±0.10	23.16±0.06	38.48±0.75	1.12±0.05
16°C, 17‰ *†	1	15.42±0.10	17.24±0.04	40.74±0.82	1.49±0.01
	2	15.77±0.08	17.05±0.05	41.60±1.37	1.45±0.02
20°C, 17‰ *	1	20.07±0.07	17.04±0.07	49.07±1.53	2.23±0.15
	2	19.99±0.08	17.02±0.07	52.34±1.03	2.43±0.11
24°C, 17‰ *	1	23.90±0.07	17.17±0.06	56.47±1.60	3.12±0.15
	2	23.89±0.06	17.05±0.05	56.83±1.46	3.17±0.14
16°C, 11‰ †	1	15.44±0.10	11.40±0.04	42.33±0.69	1.41±0.05
	2	15.41±0.01	11.40±0.03	42.58±1.13	1.41±0.07
16°C, 5‰ *†	1	15.74±0.08	5.46±0.03	42.62±0.82	1.40±0.15
	2	15.99±0.08	5.41±0.04	45.85±1.67	1.74±0.12
20°C, 5‰ *	1	20.08±0.07	5.39±0.04	50.14±0.72	2.27±0.14
	2	20.01±0.05	5.51±0.03	47.26±1.46	2.00±0.16
24°C, 5‰ *	1	23.85±0.09	5.45±0.04	58.50±1.34	2.94±0.12
	2	24.09±0.08	5.52±0.03	59.12±1.55	3.54±0.15

Note: Data are displayed as means ± standard error; #, temperature experiment; †, salinity experiment; *, temperature × salinity experiment; SL, standard length of fish.

ulated, there was some variation among tanks in several treatment groups (Table 2).

The standard length of fish and otolith weight were highly correlated (Table 1). Therefore, only one of these variables (otolith weight) was examined further. Fish that were reared in cooler temperatures had smaller otolith weights than those reared in warmer temperatures. Smaller otolith weights were also recorded for fish reared at higher salinities (single-factor experiments). There were no interactive effects between temperature and salinity on otolith weight.

Two-factor experiment

Significant interactive effects of temperature and salinity were detected for Sr:Ca, Ba:Ca, $\delta^{13}C$, and $\delta^{18}O$ concentrations in fish otoliths (Table 3; Fig. 1), and a significant effect of temperature was also detected for Mg:Ca. There were no interactive effects of temperature and salinity for Mg:Ca and Mn:Ca, although differences were detected between tanks for both Mg:Ca and Mn:Ca. The concentration ratio of Sr:Ca in otoliths increased with increasing temperature (from 16, 20, 24°C), with salinity having no effect at 16°C but significant effects at higher temperatures (SNK tests; Fig. 1*c*). The concentration ratio of Ba:Ca in otoliths also increased with increasing temperature from 16 to 20°C but did not increase between 20 and 24°C, with the exception of 30‰ (SNK tests; Fig. 1*d*). The effect of salinity on $\delta^{13}C$ and $\delta^{18}O$ isotopes in otoliths increased with increasing temperature, with significant differences detected between salinities at each temperature (SNK tests; Figs. 1*e*, 1*f*).

Backwards stepwise regression performed on Sr:Ca, Ba:Ca, $\delta^{13}C$, and $\delta^{18}O$ indicated that of the variables (temperature, salinity, ambient water chemistry, and otolith weight), only temperature and salinity influenced Sr:Ca, Ba:Ca, and $\delta^{13}C$ concentrations in otoliths, whereas temperature, ambient $\delta^{18}O$ water concentration, and otolith weight influenced $\delta^{18}O$ concentration in otoliths.

NP-MANOVA detected an interactive effect of temperature and salinity on the elemental fingerprints of Mg:Ca, Mn:Ca, Sr:Ca, and Ba:Ca in otoliths (Table 4; Fig. 2*a*) and on the isotopic fingerprints of $\delta^{13}C$ and $\delta^{18}O$ in otoliths (Table 4; Fig. 2*b*). A posteriori pairwise comparisons revealed that the elemental and isotopic compositions in otoliths of fish reared under different temperatures were significantly different from each other, but that there was greater variation among salinities as temperature increased, resulting in a significant interaction effect.

Temperature experiment at 30‰

A significant effect of temperature was detected for Sr:Ca, Ba:Ca, $\delta^{13}C$, and $\delta^{18}O$ in fish otoliths, with no significant effects detected for Mg:Ca and Mn:Ca (Table 5*a*; Fig. 3). Despite ANOVA detecting a significant difference for Sr:Ca, the post hoc SNK test initially failed to determine which treatment differed; thus, the pooling of replicate tank data

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Table 2. Summary of the water conditions within treatment tank for the three experiments.

		Trace elements								Isotopes	
Treatment	Tank	Mg (n = 3)	Mg:Ca (n = 3)	Mn (n = 3)	Mn:Ca (n = 3)	Sr (n = 3)	Sr:Ca (n = 3)	Ba (n = 3)	Ba:Ca (n = 3)	$\delta^{18}O$ (n = 3)	$\delta^{13}C$ (n = 3)
12°C, 30‰ #	1	286.67±3.33	1.23±0.00	1.36±0.19	2.37±0.32	6.23±0.03	6.79±0.04	6.83±0.13	4.75±0.09	3.30±0.10	13.55±0.35
	2	290.00±0.00	1.14±0.00	2.10±0.26	3.65±0.46	6.23±0.03	6.79±0.04	6.80±0.06	4.72±0.04	3.12±0.16	13.96±0.18
16°C, 30‰ #*†	1	290.00±0.00	1.14±0.00	2.17±0.14	3.76±0.25	6.23±0.03	6.79±0.04	7.10±0.10	4.93±0.07	3.41±0.04	11.80±0.65
	2	283.33±6.66	1.20±0.05	1.97±0.19	3.66±0.14	5.63±0.47	6.59±0.13	6.07±0.60	4.51±0.17	3.02±0.03	11.86±0.45
20°C, 30‰ #*	1	290.00±0.00	1.13±0.00	2.37±0.28	4.11±0.49	6.20±0.00	6.75±0.00	7.40±0.15	5.14±0.10	3.43±0.05	8.82±1.84
	2	286.67±3.33	1.13±0.01	2.33±0.32	4.05±0.57	6.20±0.00	6.75±0.00	6.97±0.09	4.84±0.06	3.24±0.08	12.41±0.63
24°C, 30‰ #*	1	290.00±0.00	1.34±0.00	3.13±0.37	5.44±0.64	6.27±0.03	6.83±0.04	7.30±0.12	5.07±0.08	3.09±0.40	11.19±0.24
	2	290.00±0.00	1.14±0.00	2.97±0.20	5.15±0.35	6.20±0.00	6.75±0.00	7.10±0.06	4.93±0.04	3.34±0.07	11.19±0.30
28°C, 30‰ #	1	290.00±0.00	1.11±0.00	3.03±0.18	5.15±0.30	6.40±0.00	6.81±0.00	7.63±0.15	5.18±0.10	3.24±0.28	11.45±0.34
	2	290.00±0.00	1.11±0.00	3.00±0.18	4.92±0.35	6.40±0.00	6.81±0.00	7.48±0.08	5.09±0.07	3.58±0.14	12.49±0.26
16°C, 30‰ †	1	260.00±0.00	1.35±0.01	2.27±0.42	5.21±0.93	4.43±0.03	6.40±0.06	5.27±0.12	4.86±0.16	3.03±0.29	9.48±0.33
	2	260.00±0.00	1.35±0.01	2.20±0.21	5.06±0.44	4.43±0.03	6.40±0.06	5.03±0.12	4.64±0.06	2.64±0.30	7.88±0.34
16°C, 17‰*†	1	240.00±0.00	1.65±0.00	1.77±0.07	5.37±0.20	3.20±0.00	6.10±0.00	4.07±0.09	4.94±0.11	2.15±0.26	9.50±1.46
	2	240.00±0.00	1.65±0.00	2.20±0.12	6.69±0.35	3.23±0.03	6.16±0.06	3.87±0.15	4.70±0.18	2.48±0.13	7.89±0.60
20°C, 17‰ *	1	240.00±0.00	1.60±0.02	1.47±0.09	4.35±0.30	3.37±0.03	6.24±0.02	3.93±0.03	4.66±0.10	2.65±0.33	10.47±1.13
	2	236.66±3.33	1.63±0.02	2.73±0.07	8.31±0.10	3.23±0.12	6.16±0.10	4.10±0.26	4.98±0.21	2.52±0.17	10.22±0.51
24°C, 17‰ *	1	240.00±0.00	1.65±0.00	2.30±0.25	6.99±0.76	3.23±0.03	6.16±0.06	4.37±0.03	5.31±0.04	2.58±0.15	8.23±1.18
	2	240.00±0.00	1.65±0.00	2.65±0.09	8.10±0.36	3.30±0.00	6.29±0.00	4.60±0.12	5.67±0.16	2.37±0.23	9.02±0.83
16°C, 11‰ †	1	193.33±6.67	2.13±0.07	1.47±0.18	7.11±0.56	1.97±0.13	6.00±0.01	2.60±0.21	5.05±0.12	2.05±0.05	7.47±2.20
	2	196.67±3.33	2.12±0.08	1.00±0.00	4.76±0.10	2.10±0.00	6.27±0.13	2.60±0.06	4.95±0.15	1.64±0.29	6.59±0.45
16°C, 5‰ *†	1	120.00±0.00	2.87±0.04	1.20±0.10	12.66±0.86	0.93±0.01	6.14±0.02	1.63±0.20	6.89±0.76	2.37±0.77	4.52±1.05
	2	120.00±0.00	2.90±0.04	1.03±0.03	11.04±0.40	0.92±0.01	6.16±0.02	1.33±0.03	5.70±0.17	1.21±0.13	5.77±0.52
20°C, 5‰ *	1	126.67±3.33	2.85±0.01	1.20±0.01	11.90±0.74	0.98±0.02	6.11±0.01	1.67±0.13	6.61±0.40	1.48±0.15	6.52±1.26
	2	130.00±0.00	1.62±0.05	1.00±0.00	9.78±0.16	0.97±0.01	6.05±0.05	1.97±0.37	7.72±1.55	1.35±0.15	5.95±0.73
24°C, 5‰ *	1	130.00±0.00	2.85±0.07	1.63±0.29	15.96±3.18	0.99±0.01	5.99±0.07	2.50±0.06	9.69±0.04	1.68±0.18	6.68±0.63
	2	130.00±0.00	2.83±0.05	2.37±0.32	22.95±3.54	0.99±0.01	5.99±0.06	2.53±0.13	9.76±0.37	1.44±0.15	4.03±1.54

Note: Data are displayed as means ± standard error, where errors of 0.00 represent identical replicate samples; #, temperature experiment; †, salinity experiment; *, temperature × salinity experiment. Units: Mg, Sr (mg·L^{-1}); Mn, Ba (μg·L^{-1}); Mg:Ca (mol·mol^{-1}); Mn:Ca and Ba:Ca (μmol·mol^{-1}); Sr:Ca (mmol·mol^{-1}); $\delta^{13}C$ and $\delta^{18}O$ (‰).

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Table 3. Results of analysis of variance (ANOVA) comparing the elemental ratio and isotopic concentrations in otoliths among temperature (T) and salinity (S) treatments (two-way manipulation).

Source	df	MS Mg	MS Mn	MS Sr	MS Ba	MS $\delta^{13}C$	MS $\delta^{18}O$
Temperature	2	14 552.72**	6.775	593 845.24**	33.279***	47.799***	22.918***
Salinity	2	1 222.28	0.627	9 306 157.87***	4.802**	15.229***	28.637***
Tank (T × S)	9	1 391.99*	3.616***	71 662.77	0.468	0.164	0.079*
T × S	4	89.44	0.570	1 293 878.98***	2.922*	1.223**	1.665***
Residual	108	699.64	1.002	68 390.14	0.424	0.135	0.036

Note: Cochran's *C* tests were used to test homogeneity of variance; all tests were nonsignificant. For this table, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

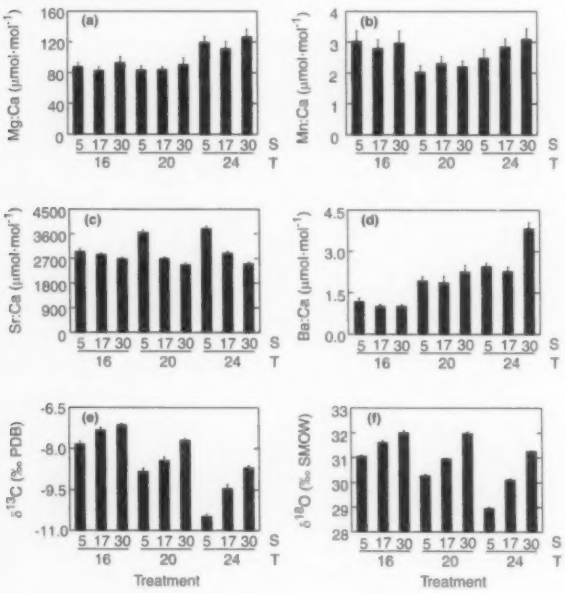

Fig. 1. Mean concentrations (± standard error (SE)) of (*a*) Mg, (*b*) Mn, (*c*) Sr, (*d*) Ba, (*e*) $\delta^{13}C$, and (*f*) $\delta^{18}O$ in otoliths of black bream (*Acanthopagrus butcheri*) reared under experimental treatments of temperature and salinity (two-way manipulations). S, salinity of the rearing water in ‰; T, temperature of the rearing water in °C. Carbon isotope concentrations are standardized to Peedee belemnite (PDB) and oxygen isotope concentrations are standardized to standard mean ocean water (SMOW).

was done to increase the power of the test and to allow for differences to be determined (Underwood 1999). This analysis was achieved by pooling the mean squares of the interaction term with the residual (Winer et al. 1991). The concentration ratio of Sr:Ca in otoliths was significantly greater at low and high temperatures (12 and 16°C and 28°C, respectively) compared with intermediate temperatures (20 and 24°C), where the concentration ratio was lower (SNK tests; Fig. 3*c*). Significant differences were observed for Ba:Ca for the 16, 20, and 24°C treatments, where Ba:Ca concentration ratio increased with temperature but the upper two (24 and 28°C) and lower two (12 and 16°C) treatments showed no significant differences (SNK tests; Fig. 3*d*). The concentration of $\delta^{13}C$ decreased as temperature increased, with significant differences found among the four higher temperatures (16, 20, 24, 28°C) and no difference detected between 12 and 16°C (SNK tests; Fig. 3*e*). Significant differences were observed for $\delta^{18}O$ between 12 and 16°C and again between 20, 24, and 28°C, with a general trend for a decrease in $\delta^{18}O$ with increasing temperature (no differences were detected between 12 and 20°C treatments and again between 16 and 20°C treatments) (SNK tests; Fig. 3*f*).

Backwards stepwise regression for Sr:Ca and Ba:Ca indicated that of the variables (temperature, ambient water chemistry, and otolith weight), only temperature influenced the Sr:Ca and Ba:Ca concentration ratios in otoliths. Backwards stepwise regression analysis performed on $\delta^{13}C$ and $\delta^{18}O$ isotopes indicated that temperature, ambient $\delta^{13}C$ water concentration, and otolith weight influenced the concentration of $\delta^{13}C$ in otoliths, whereas otolith weight influenced $\delta^{18}O$ concentration in otoliths.

NP-MANOVA detected a significant effect of temperature on the elemental fingerprints of Mg:Ca, Mn:Ca, Sr:Ca, and Ba:Ca in otoliths (Table 4; Fig. 2*c*) and the isotopic fingerprints of $\delta^{13}C$ and $\delta^{18}O$ (Table 4; Fig. 2*d*). A posteriori pairwise comparisons revealed differences in the elemental fingerprints between 16, 20, and 24°C, although the two lower (12 and 16°C) and two higher (24 and 28°C) treatments showed no significant differences (Fig. 2*c*). A posteriori pairwise comparisons revealed no difference in the isotopic fingerprints between 12 and 16°C, whereas significant differences were observed at higher temperatures (Fig. 2*d*).

Salinity experiment at 16°C

There were no significant effects of salinity on the concentration ratios of any elements in the fish otoliths (Table 5*b*). Significant tank effects were recorded for Mg:Ca, Mn:Ca, and Ba:Ca, indicating variation between replicate treatment tanks (Table 5*b*; Fig. 4). A significant effect of salinity was detected for $\delta^{13}C$ and $\delta^{18}O$ (Table 5*b*; Figs. 4*e*, 4*f*). Backwards stepwise regression performed on carbon and oxygen isotopes indicated that of the variables (salinity, ambient water chemistry, and otolith weight), only salinity influenced the concentrations of $\delta^{13}C$ and $\delta^{18}O$ in otoliths.

Nonparametric analysis of variance did not detect any significant effect of salinity on the elemental fingerprints in otoliths (Table 4; Fig. 2*e*), although a significant tank effect was detected, again suggesting variability between replicate tanks. A multidimensional scaling plot of element centroids from each tank demonstrates the similarity among treatment groups and shows the high degree of variability between replicate tanks (Fig. 2*e*). A significant effect of salinity on the isotopic fingerprints of $\delta^{13}C$ and $\delta^{18}O$ in otoliths was detected (Table 4; Fig. 2*f*). A posteriori pairwise comparisons revealed differences in the isotopic fingerprints between the low salinities (5 and 11‰) and high salinities (17, 23, 30‰)

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Table 4. Results of nonparametric multivariate analysis of variance (NP-MANOVA) comparing multi-element and -isotope fingerprints in otoliths among treatments of the temperature and salinity experiment and the temperature and the salinity experiments alone.

Experiment	Source	df	MS elements	MS isotopes
Temperature × salinity (two-way)	Temperature	2	5.720***	2.870***
	Salinity	2	1.436***	1.057***
	Temperature × salinity	4	0.364*	0.185***
	Residual	117	0.196	0.019
Temperature (one-way)	Temperature	4	3.191***	0.893***
	Tank (temperature)	5	0.277	0.005
	Residual	60	0.202	0.008
Salinity (one-way)	Salinity	4	0.153	0.129***
	Tank (salinity)	5	0.693**	0.002
	Residual	60	0.194	0.010

Note: All data were transformed to $\ln(X + 1)$ before analysis. For this table, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

(Fig. 2*f*), seen with an increased concentration of $\delta^{13}C$ and $\delta^{18}O$ with increasing salinity.

Discussion

Interactive effects of temperature and salinity

Temperature and salinity interacted to influence Sr:Ca, Ba:Ca, $\delta^{13}C$, and $\delta^{18}O$ (and the combined elemental and isotopic fingerprints) in black bream otoliths. The influence of salinity on the elemental ratio and isotopic concentrations also generally increased with increasing temperature. Interactive effects of temperature and salinity on the elemental ratio and isotopic concentrations in otoliths have rarely been reported. Secor et al. (1995) detected a significant interactive effect of temperature and salinity on Sr concentration, but the biological significance of this is difficult to interpret because of the unnaturally low Sr concentrations in the artificial seawater used in their experiment.

The results of the present study suggest that the choice of temperature and salinity treatments may explain why the interactive effects of these factors have not been detected in previous experiments. A strong interactive effect between temperature and salinity on Sr:Ca was detected when comparing higher (i.e., 20 and 24°C) with lower temperatures (i.e., 16°C), but comparison of the two high temperatures (20 and 24°C) did not yield this interaction. Thus, the treatments chosen by Tzeng (1996) of two high temperatures (23 and 28°C) and by Chesney et al. (1998) of three high salinities (20, 26, and 33.4‰) may not have been broad enough to detect interactive effects on elemental concentrations. In other studies, interactive effects of temperature and salinity on elements in otoliths were not detected as they were not analyzed to detect such effects (Kawakami et al. 1998) or because of the loss of all fish from one treatment, reducing the experiment to a single-factor design (Fowler et al. 1995*a*, 1995*b*).

Effects of temperature

The single-factor experiments in the current study revealed that the concentration ratio of the elements Sr:Ca and Ba:Ca and concentrations of isotopes $\delta^{13}C$ and $\delta^{18}O$ were significantly affected by temperature, whereas Mg:Ca and Mn:Ca concentration ratios were not. Furthermore, the combined elemental fingerprint of Mg:Ca, Mn:Ca, Sr:Ca, and Ba:Ca and the combined isotopic fingerprint of $\delta^{13}C$ and $\delta^{18}O$ both showed significant effects owing to temperature. The concentration ratio of Sr:Ca in otoliths was greater at the two extreme temperature treatments (12 and 28°C), whereas the concentration ratio of Ba:Ca increased with increasing temperature. Both $\delta^{13}C$ and $\delta^{18}O$ concentrations decreased with increasing temperature, although the trends were nonlinear.

The result that Sr:Ca concentration ratio in otoliths was greater at low (12°C) and high (28°C) temperatures and was reduced at mid-range temperatures (20–24°C) may help to explain the variation of results reported in several independent experiments. Experiments that have detected a positive effect on Sr with temperature reared fish at high temperatures (i.e., 20°C and above) (Hoff and Fuiman 1993, 1995; Bath et al. 2000), whereas those that detected negative effects reared fish at low temperatures (i.e., 17°C and below) (Townsend et al. 1992, 1995). However, there are experiments that do not conform to these trends, such as Kalish (1989), who detected a slight increase in Sr:Ca with temperature using treatments of 13, 16, 19, and 22°C. In addition, Tzeng (1996) and Kawakami et al. (1998) detected no effect of temperature (23 and 28°C and 12, 17, 22, and 27°C, respectively) on otolith Sr:Ca. However, both experiments that detected no effect used the same species of eel, *Anguilla japonica*, and it is possible that temperature may influence the concentration ratio of Sr:Ca differently in different species. If previous studies had used broad ranges of temperatures, then the results of the literature may be more consistent. We recommend that future experiments focus on a broad range of temperatures, or at least the entire range experienced by the species, and be designed to test for interactions between environmental factors.

The concentration ratio of Ba in otoliths increased with temperature in the current study, which is in contrast to the nonsignificant effect of temperature on barium concentration ratio detected by previous studies (e.g., Fowler et al. 1995*a*, 1995*b*; Bath et al. 2000). The greatest effect was over the temperature range of 16 to 24°C, and no effect was detected between the highest temperatures of 24°C and 28°C. The limited temperature ranges investigated by both Fowler et al. (1995*a*, 1995*b*) and Bath et al. (2000) of 20 and 25°C may explain why they did not detect an effect.

The nonsignificant effect of temperature on Mn:Ca con-

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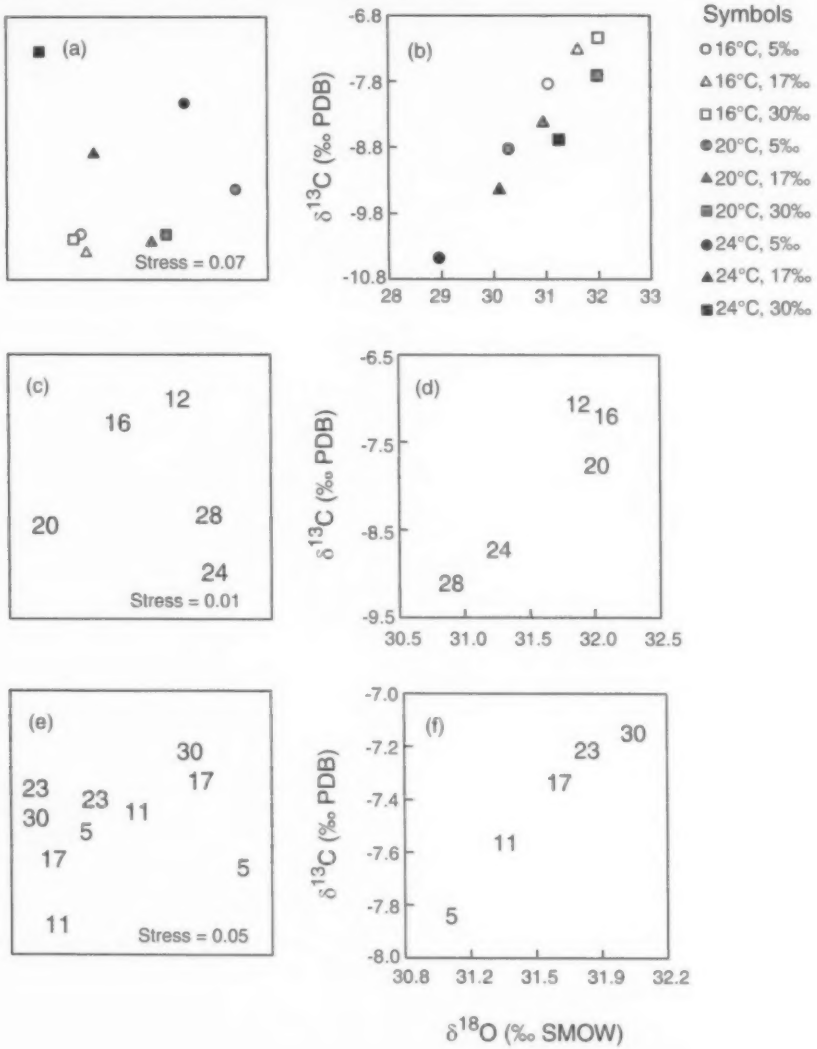
Fig. 2. Plots summarizing the variation in elemental and isotopic fingerprints of otoliths from black bream (*Acanthopagrus butcheri*) reared under experimental treatments. Nonmetric multidimensional scaling (MDS) ordinations comparing centroids of treatment groups of (*a*) temperature and salinity (two-way) manipulations (stress = 0.07), (*c*) temperature manipulations (stress = 0.01), (*e*) salinity manipulations (stress = 0.05); these plots are only determined to within an arbitrary orientation, reflection, location, and scale, which explains the absence of axis scales and labels in the figures. Plots of carbon versus oxygen isotope concentration comparing the means of each treatment group of (*b*) temperature and salinity (two-way) manipulations, (*d*) temperature manipulations, and (*f*) salinity manipulations. In *c* and *d*, numbers = temperature (°C), and in *e* and *f*, numbers = salinity (‰).



tradicts the only other experimental results for manganese. Fowler et al. (1995*a*) found a reduction in Mn concentration at higher temperatures using solution-based analysis. In the current experiment, variability in Mn concentration of otoliths between replicate tanks of each treatment was high, and differences between treatments were not detected. Experiments investigating the effects of temperature on Mg have shown both significant effects (Fowler et al. 1995*a*, 1995*b*), with Mg concentration decreasing with increasing temperature, and nonsignificant effects (Hoff and Fuiman 1995). In the current experiment, Mg:Ca was highly variable in concentration between otoliths from individual fish in each tank, as well as between replicate tanks of each treatment. Thus, the large variations in Mn:Ca and Mg:Ca concentration ratios detected in the current study suggest that these particular elements may not be applicable for use in otolith microchemistry studies involving temperature and salinity, in contrast to Sr:Ca and Ba:Ca, which yield clearer results.

The linear relationship between $\delta^{13}C$ and $\delta^{18}O$ and temperature has previously been described with some degree of

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Table 5. Analysis of variance (ANOVA) comparing the elemental ratio and isotopic concentrations in otoliths among (*a*) temperature treatments (T) and (*b*) salinity treatments (S).

	Source	df	MS Mg	MS Mn	MS Sr	MS Ba	MS $\delta^{13}C$	MS $\delta^{18}O$
(*a*)	Temperature	4	4610.270	2.694	173 649.503**	26.227***	0.145***	3.735***
	Tank (T)	5	1582.526	2.427	32 664.084	0.055	0.001	0.030
	Residual	60	940.244	1.401	37 975.092	0.519	0.001	0.070
(*b*)	Salinity	4	254.772	0.841	0.024	0.027	1.124***	1.976**
	Tank (S)	5	1989.666**	5.530**	0.008	0.076*	0.017	0.093
	Residual	60	559.783	1.338	0.009	0.029	0.079	0.047

Note: Cochran's *C* tests were used to test homogeneity of variance. All tests were nonsignificant except $\delta^{13}C$ (temperature), which was transformed to $\ln(X + 1)$. For this table, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Fig. 3. Mean concentrations (± standard error (SE)) of (*a*) Mg, (*b*) Mn, (*c*) Sr, (*d*) Ba, (*e*) $\delta^{13}C$, and (*f*) $\delta^{18}O$ in otoliths of black bream (*Acanthopagrus butcheri*) reared under experimental treatments of temperature. Carbon isotope concentrations are standardized to Peedee belemnite (PDB) and oxygen isotope concentrations are standardized to standard mean ocean water (SMOW). Graphs with letters above bars indicate similarity between treatments; graphs with n/s indicate that there are no significant effects between treatments.

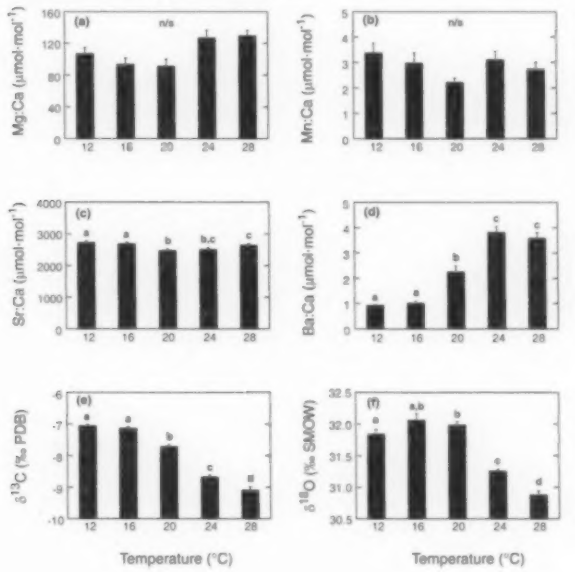
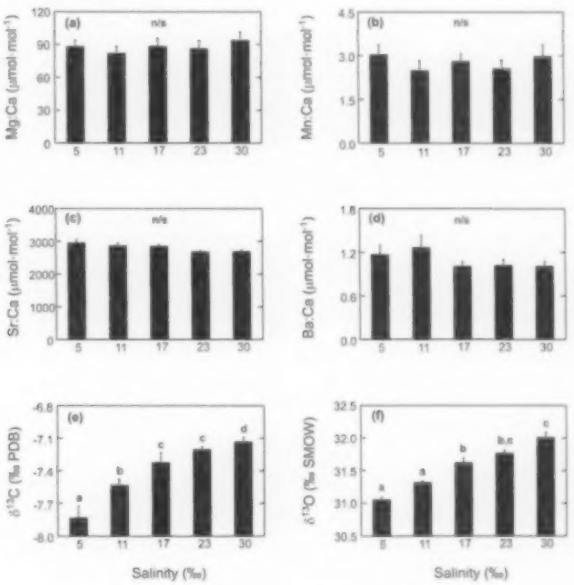


Fig. 4. Mean concentrations (± standard error (SE)) of (*a*) Mg, (*b*) Mn, (*c*) Sr, (*d*) Ba, (*e*) $\delta^{13}C$, and (*f*) $\delta^{18}O$ in otoliths of black bream (*Acanthopagrus butcheri*) reared under experimental treatments of salinity. Carbon isotope concentrations are standardized to Peedee belemnite (PDB) and oxygen isotope concentrations are standardized to standard mean ocean water (SMOW). Graphs with letters above bars indicate similarity between treatments; graphs with n/s indicate that there are no significant effects between treatments.



variation (see Kalish 1991*b*) and has formed the basis of many predictive equations (Kalish 1991*a*, 1991*b*; Thorrold et al. 1997) extensively used in fisheries ecology (e.g., Edmonds et al. 1999) and palaeoecology (e.g., Patterson 1999) for reconstructing past temperatures. The results of the current study support the use of such equations, although the relationships detected in this study were not always linear and the magnitude of the relationship changed with salinity. Our work gives some insight into why slight variations of this equation may occur. Previous studies by Kalish (1991*a*), who reared fish at 38.4‰, and Thorrold et al. (1997), who reared fish at 30‰, showed variations in the $\delta^{18}O$–temperature relationship that may have been due to salinity. Slight variations of the equation may also be due to rearing temperature, for example, Kalish (1991*a*) reared fish at 13, 16, 19, and 22°C and Thorrold et al. (1997) reared fish at 18, 20.5, 22.5, and 25°C.

Biological factors such as kinetics may be the underlying reason as to why temperature effects on otolith chemistry are detected (Kalish 1989). Kinetic effects in otoliths are thought to manifest as changes in the proteinaceous compounds surrounding the otolith (e.g., Brown and Severin 1999). These proteins are likely to be indirectly affected by temperature and hence may result in changes to the otolith crystal morphology from the normal aragonite structure to vaterite, which has been shown to affect uptake of elements into otoliths (e.g., Brown and Severin 1999). Greater knowledge of influence of kinetics on otolith microchemistry may lead to a more de-

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tailed explanation as to why otolith microchemistry changes with temperature treatments.

Effects of salinity

The concentration ratios of individual elements in otoliths of *A. butcheri* showed no relationship with salinity, whereas $\delta^{13}C$ and $\delta^{18}O$ concentrations displayed a strong positive relationship. Similarly, the combined elemental fingerprint of Mg:Ca, Mn:Ca, Sr:Ca, and Ba:Ca displayed no trends with salinity; however, the isotopic fingerprints of $\delta^{13}C$ and $\delta^{18}O$ had a positive relationship with salinity. When temperature was constant, the concentrations of $\delta^{13}C$ and $\delta^{18}O$ in otoliths appeared to be primarily due to an effect of rearing-water salinity.

The results from the single-factor salinity experiment agree with prior experiments that found no effects of salinity on Sr and Mg (Hoff and Fuiman 1995; Chesney et al. 1998) and Mn and Ba (Fowler et al. 1995*b*) in otoliths. However, there were significant salinity effects detected for Sr and Ba at 20 and 24°C in the two-factor experiment. Thus, the temperature at which the single-factor experiment was done in this study (16°C) appeared to be too low to detect any salinity effects. The results of Tzeng (1996) seem to support this claim, with differences in Sr:Ca detected among salinity treatments at high temperatures (22–23 and 27–28°C), although Fowler et al. (1995*b*), Hoff and Fuiman (1995), and Chesney et al. (1998), who also reared fish at high temperatures (20°C and above), found no salinity effects on elemental concentrations in otoliths. Therefore, the ability to draw reliable conclusions regarding the effect of salinity alone on otolith elemental concentration ratios is impeded by the variable results reported between studies, and hence further investigation is required. The effects of salinity on isotopic concentrations in fish otoliths have not been previously investigated, and further independent analyses are required for their validation.

Other factors influencing otolith microchemistry

Although it is necessary to determine the influence of temperature and salinity on otolith microchemistry if otoliths are to be used to reconstruct migratory patterns or temperature and salinity histories of fish, it is equally important to recognize factors other than these that may affect the incorporation of elements and isotopes into otoliths. The microchemistry of the surrounding water has been demonstrated to influence the concentrations of elements and isotopes in otoliths (e.g., Thorrold et al. 1997; Bath et al. 2000; Milton and Chenery 2001). In the current study, although the concentration of isotopes in otoliths was influenced by that of the water, this effect was minimal compared with that of temperature and salinity. The fact that elemental concentration ratios in otoliths were not affected by that of the water may be explained by the smaller range in elemental concentration ratios among treatment groups compared with studies such as that of Bath et al. (2000), who found significant effects of water chemistry.

Biological factors, such as metabolism, kinetics, and ontogeny, are thought to influence otolith microchemistry (Kalish 1989). Sadovy and Severin (1994) reported that the concentration ratio of Sr:Ca in fish otoliths was inversely related to the growth rate of the fish. In the current study, fish growth (as indicated by otolith weight) was positively affected by rearing temperature. There was also a relationship between both carbon and oxygen isotopic concentration in the otolith and otolith weight. The relative differences in fish growth rates between treatments cannot be ruled out as a factor influencing otolith microchemistry. Similarly, concentrations of Sr, Ba, and Mg in otoliths have been shown to vary with ontogeny (Fowler et al. 1995*b*). Ontogenetic factors are unlikely to have affected otolith microchemistry in the current study as all of the fish were the same age and from the same brood stock.

Applications

The ability to reconstruct aspects of the life history of a fish (e.g., migratory patterns) using otoliths relies largely on predictive responses of otolith microchemistry to ambient temperature and salinity. Kafemann et al. (2000) and Secor et al. (2001) have both used the concentration ratio of Sr:Ca in fish otoliths to reconstruct migratory patterns based on salinity profiles of the water. These studies collected fish from different salinity environments (e.g., freshwater and brackish) and, after analysis of the otoliths, have charted possible migratory patterns of the fish along large rivers (up to 250 km; Secor et al. 2001) varying in salinity from brackish to oceanic. Similarly, Edmonds et al. (1999) reconstructed the salinity histories of fish from a large bay based on isotopic concentrations in otoliths. It is logical to assume that coastal regions such as rivers and bays may vary in both temperature and salinity simultaneously. Thus, the reconstruction of migratory patterns based solely on the salinity effects on otolith microchemistry (without taking into account possible interactions of salinity with temperature) may result in incorrect interpretations of fish migratory patterns. Conversely, in areas where only temperature or salinity vary, such as in open oceans where salinity may remain relatively constant over large areas yet temperature changes markedly, the use of single-factor reconstructions of migratory patterns may be more reliable.

In conclusion, differences in elemental and isotopic concentrations of otoliths appear to be strongly affected by both water temperature and salinity. Importantly, these results suggest that although single-factor tests of environmental processes provide quantitative information if their effects are independent, they cannot predict the interactive effects of multiple factors. This point is especially significant where variables are not independent of one another, as for temperature and salinity of seawater. The results presented here suggest that otolith microchemistry may be a useful tool for studying and reconstructing the temperature and salinity life histories of fish. The potential applications include accurate predictions of fish migratory patterns.

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Energetic costs of migration through the Fraser River Canyon, British Columbia, in adult pink (*Oncorhynchus gorbuscha*) and sockeye (*Oncorhynchus nerka*) salmon as assessed by EMG telemetry

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Abstract: Adult Pacific salmon (*Oncorhynchus* spp.) depend on energy reserves to complete their upriver spawning migration. Little is known about how flow patterns and bank characteristics affect energetics or how species differ in reach-specific energy use. In 1999, electromyogram (EMG) radiotelemetry was used to describe activity levels and estimate energy use of 12 adult pink salmon (*Oncorhynchus gorbuscha*) during their upstream migration in a 7-km section of the Fraser River Canyon. Data collected previously on sockeye salmon (*Oncorhynchus nerka*) in the same study area provided a species comparison. We could not identify any strong differences in energetics between species. Although sex had some influence, reach characteristics were the primary factors affecting migration activity and energetics. Fish increased their activity levels when they migrated through reaches constricted by islands or gravel bars compared with nonconstricted reaches. The former contained higher velocity currents and more complex hydraulic conditions than the latter. Two behavioural responses, with similar energetic consequences, occurred in constricted reaches. Either fish swam slowly and took more time, presumably searching for lower velocity areas for migration thus increasing passage time, or they swam quickly through higher velocity flow fields.

Résumé : Les saumons du Pacifique (*Oncorhynchus* spp.) adultes utilisent leurs réserves énergétiques lors de leurs migrations de fraye vers l'amont des rivières. On connaît encore mal les conséquences énergétiques des patterns de courant et des caractéristiques des berges, ainsi que l'utilisation de l'énergie chez les différentes espèces dans les sections particulières du cours d'eau. En 1999, l'électromyographie (EMG) par radio-télémétrie nous a permis de décrire les niveaux d'activité et d'estimer l'utilisation de l'énergie chez 12 saumons roses (*Oncorhynchus gorbuscha*) durant leur migration vers l'amont dans une section de 7 km du canyon du Fraser. Des données récoltées antérieurement sur le saumon rouge (*Oncorhynchus nerka*) dans la même région d'étude ont servi de point de comparaison pour établir les différences inter-spécifiques. Aucune différence importante n'est apparue dans la dynamique énergétique entre les deux espèces. Bien que le sexe du poisson ait une influence, ce sont les caractéristiques de la section de la rivière qui affectent le plus la migration et l'utilisation de l'énergie. Les poissons augmentent leur niveau d'activité lorsqu'ils traversent des sections rétrécies par la présence d'îles ou de bancs de gravier, par comparaison aux sections non rétrécies. Les sections rétrécies contiennent des courants plus forts et des conditions hydrauliques plus complexes que les autres. Deux réactions comportementales, à incidences énergétiques semblables, se produisent dans les sections rétrécies. Les poissons nagent lentement et mettent plus de temps à leur migration, sans doute parce qu'ils recherchent des points de courant plus faible et ainsi ils augmentent la durée de leur passage, ou alors ils nagent rapidement à travers les champs de courant plus rapide.

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Introduction

Upriver migration of anadromous fish can be energetically expensive, particularly when travel distances are long and river environmental conditions adverse (Bernatchez and Dodson 1987; Brett 1995; Leonard and McCormick 1999). Body constituent analyses on Pacific salmon (*Oncorhynchus* spp.) reveal that depending on migratory conditions, more than 50% of body energy may be used to complete migration (reviewed by Brett 1995). Such high levels of energy depletion are thought to cause en route or prespawning mortality (Rand and Hinch 1998; Hinch and Bratty 2000; Macdonald 2000). However, very little is known about the mechanisms responsible for high levels of energy use. Constituent analyses provide only a coarse-grained measure of how a stock uses its energy reserves and cannot be used to measure how specific habitat features influence energy use. Because fish must be killed to measure body energy, different individuals must be examined each time; therefore, the influence of behaviour or morphology cannot be evaluated by this method. By contrast, electromyogram (EMG) radiotelemetry enables one to quantify swimming speeds of individual migrating fish and thus provide fine-scale information on energy-use patterns (McKinley and Power 1992; Hinch et al. 1996).

EMG telemetry has been used for several years to investigate the factors responsible for variability in migratory energetics of sockeye salmon. Earlier research found that sex, size, and individual swimming speed patterns are important factors affecting energy use (Hinch et al. 1996; Hinch and Rand 1998; Hinch and Bratty 2000). Physical habitat features have also proven to significantly influence sockeye energy use. Specifically, river constrictions and their associated multidirectional currents appear to cause relatively high passage costs (Hinch et al. 1996; Hinch and Rand 1998). However, there has been little investigation into the behaviour and energetics of other salmon species during their upriver spawning migrations.

Our first objective was to use EMG telemetry to estimate swimming speeds, ground speeds, and energy use of adult pink salmon (*Oncorhynchus gorbuscha*) during their migration through the Fraser River Canyon. We predict that as previously found with sockeye, female pink salmon will be more energetically efficient than males and that river constrictions will increase energy expenditures. The second objective was to compare pink salmon swimming energetics with those of sockeye salmon (*Oncorhynchus nerka*), previously described by Hinch and Rand (1998). To effectively make this comparison, a reanalysis of those data was required. Pink salmon are believed to be weaker swimmers than sockeye (Brett 1982) and, in particular, are thought not to be adept at negotiating high velocity barriers because of their relatively small body size (Heard 1991). We therefore predict that pink salmon will be less efficient in their use of energy for swimming during migration compared with sockeye salmon.

Materials and methods

Calibrating EMG signals to swimming speeds

A description of the EMG radio transmitters (Lotek Engineering, Newmarket, Ont.) and specific details about their surgical implantation are outlined in Hinch et al. (1996). EMG transmitters are surgically implanted into a fish's abdomen. Sensing electrode tips are positioned approximately 1.0 cm apart, secured below the dorsal fin in the lateral red muscle. Although this muscle type is used primarily in steady, nonbursting aerobic swimming, the electrodes are also sensitive to contractions of the relatively larger white muscle (Hinch et al. 1996; Hinch and Rand 1998), which is recruited primarily during burst, anaerobic swimming. Intervals between EMG signals (termed EMG pulse intervals or EMGPI, measured in milliseconds, ms) are thus associated with tail beat frequency (TBF) and hence with swimming speed across the full range of aerobic and anaerobic speeds (Hinch and Rand 1998; Hinch and Bratty 2000).

We followed a two-step process to convert EMGPI values from pink salmon into estimates of swimming speed; a similar approach was used on sockeye salmon by Hinch and Rand (1998). The first step was to generate mathematical relationships for both sexes between EMGPI and TBF. To accomplish this, in October 1999, eight adult pink salmon, four males (fork length, 47.2–55.2 cm; mass, 1.25–2.00 kg) and four females (fork length, 49.6–55.0 cm; mass, 1.00–1.75 kg), were collected using dip nets from the fish ladder at the Seton Lake dam near Lillooet, British Columbia (B.C.; Fig. 1), and were implanted with EMG transmitters. These fish then swam in a large swimming tunnel following the methodology described in Jain et al. (1997). A detailed description and photographs of the tunnel and its components are provided at http://www.sfu.ca/biology/faculty/farrell/swimtunnel/swimtunnel.html. The tunnel has a volume of 471.2 L and was capable of creating water velocities up to 150 $cm \cdot s^{-1}$. However, we were able to record swimming speeds in the tunnel that were much greater than this because salmon often do not swim at a constant pace in swimming tunnels (e.g., they accelerate and decelerate), particularly at the higher water velocities and as they get more fatigued. We were able to generate EMGPI values in the tunnel that spanned the complete range of EMGPI values observed in the field. This is elaborated on in the results.

We recorded EMGPI and TBF data in the following manner. Individual fish were placed in the swimming tunnel and exposed, at sequential intervals, to water velocities that increased incrementally at 0.15 body lengths per second ($BL \cdot s^{-1}$). The intervals were 5–20 min in length and a trial lasted until the fish was exhausted and could not get off the rear grid. We were not interested in measuring oxygen consumption or relating water speed to EMGPI, so interval length did not matter. Our goal was simply to observe a range of EMGPI values that would be similar to that exhibited by migrating fish carrying transmitters. A stereo video camera system synchronously recorded onto a single video image the swimming fish and the digital face of the EMG radio receiver (model SRX 400; Lotek Engineering). The radio receiver displayed every EMGPI transmitted from the fish, usually 1–$2 \cdot s^{-1}$. In the laboratory, after the field telemetry study was completed, we viewed the videotapes in slow motion and located instances when fish were swimming in the centre of the tunnel and were being propelled by a complete tail beat (i.e., one complete oscillation of the caudal peduncle); observations were not considered if fish were near the tunnel wall or back grid. EMGPI values clearly associated with the initiation of a tail beat were transcribed. Because the cam-

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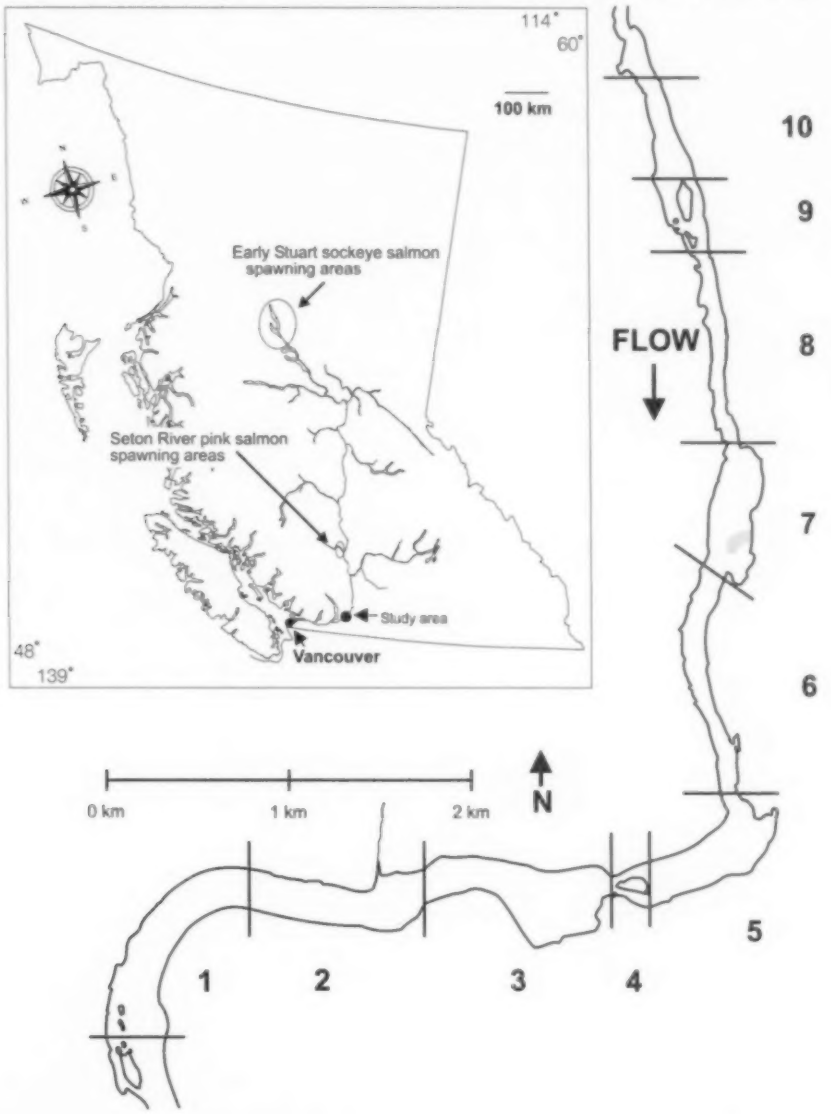
Fig. 1. Map of Fraser River Canyon indicating the nine study reaches (numbered). Inset is a map of British Columbia, Canada, showing the Fraser River and its main tributaries, the locations of spawning destinations for the two stocks of salmon in this study, and the location of the canyon study area (tip of arrow head). Seton Dam located at western end of pink salmon (*Oncorhynchus gorbuscha*) spawning area.



eras record 60 images·s^{-1}, we could calculate TBF associated with the EMGPI value by counting the number of video frames required to complete the tail beat. For each fish, we developed a relationship between EMGPI values and TBF by transcribing approximately 100 EMGPI values from the videotapes. We ensured that the range of transcribed EMGPI values for each fish was at least as great as that observed from the field telemetry EMGPI values (ranges provided in Results).

The second step in estimating swimming speeds from EMGPI values was to use an equation from Brett (1995). He had adult pink salmon swim in a 184 cm wide, open flume and used movie cameras to record TBF and demonstrated a linear relationship between swimming speeds and TBF. His relationship would much better reflect reality than anything we could generate in our swimming tunnel, despite its relatively large size, because of the phenomenon of solid blocking and wall effects within a tunnel. We used his equation (swimming speed (cm·s^{-1}) = 0.739TBF (beats·min^{-1}) + 14.904; $P < 0.0001$; $r^2 = 0.64$; standard error (SE) intercept = 22.513; SE slope = 0.121) to predict instantaneous swimming speeds from individual TBF values.

Telemetry study

The Fraser River Canyon, situated in the southwest corner of British Columbia (Fig. 1), exhibits a diversity of flow

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conditions and habitat features that create challenges for upriver passage of salmon (Hinch and Rand 1998; Hinch and Bratty 2000). The study area in the Fraser River Canyon was from kilometre 150 to 157, the same as that used by Hinch and Rand (1998). Reach length, width, and gradient were determined using 1:4000 air photos. Reaches 1 and 2, located immediately downstream of the canyon, had an average gradient of 75 cm·km^{-1}. All other reaches were in the canyon and had an average gradient of 120 cm·km^{-1}. Reaches ranged in length from 200 to 1100 m and in width from 50 to 500 m. Surface water speeds along the centre line of each reach were estimated by timing the passage of wooden blocks (20 cm × 20 cm × 5 cm) over a known distance in the main current of the river. Blocks were floated during the middle of our study when discharge was about the same for both years. These values are intended to provide one, albeit coarse, measure of the broad differences in flow features that exist among reaches and are not intended to reflect the specific current speeds that salmon encounter while migrating. We subjectively classified reach bank morphology by the presence of parallel banks (termed "straight"), large bends (termed "bend"), or features (e.g., large islands, gravel bars) that cause flow constrictions (termed "constriction").

During September and October 1999, six male pink salmon (fork length, 47.5–56.6 cm; mass, 1.50–2.25 kg) and six female pink salmon (fork length, 47.5–50.6 cm; mass, 1.00–1.35 kg) were collected from a fish wheel situated 200 m downstream of the study area, and transmitters were implanted at that site. The wheel was operated by the Yale First Nations Band (Yale, B.C.). Fish were held in a pen near the wheel for at least 1 h to recover from the surgery. Fish were released into a large slow water eddy at the edge of the river mainstem near the holding pen and individually tracked upstream using a hand-held directional three element Yagi antenna and EMG receiver. Only one fish was released per day and we tried to alternate sexes from one day to next. Fish were tracked by following them on foot along the river banks, and their positions could be ascertained to within 5 m (determined previously at our study sites using transmitters suspended on submerged lines at known depths (Hinch et al. 1996)). Migration time was measured as the amount of time it took a fish to swim through a reach from first entry to first exit. We found that pink salmon stopped their forward migration at dusk and did not migrate at night, so times from dusk to dawn were not included in the migration time. Ground speed was calculated by dividing the migration time by the reach length.

EMGPI values were recorded by the receivers at an interval of every 3–5 s. Each EMGPI value was converted to TBF in beats per second using the linear regression equations developed from the swimming tunnel trials (equations given in Results). Each TBF value was converted to an estimate of instantaneous swimming speed using the relationship developed by Brett (1982) and described above. Assuming receivers record an EMGPI value every 4 s and a reach takes 60 min to traverse, we would accumulate 900 EMGPI values and hence have 900 estimates of swimming speeds. These estimates of swimming speeds were averaged for each fish within reach. Individual specific energy use was estimated using a salmon bioenergetics model with variables average swimming speed through the reach, average river temperature, fish mass, and migration time through the reach (Hinch and Rand 1998). This model was originally developed by Beauchamp et al. (1989) and parameterized using adult sockeye salmon. A comparable model for adult pink salmon has not been developed.

Hinch and Rand (1998) used EMG transmitters to track five male and five female early Stuart sockeye salmon in 1993 through the same reaches described above. Using results from laboratory swimming experiments and the other approaches described above, they collected ground and swimming speeds and estimated reach specific energy expenditures. It is these data that are used for making comparisons with pink salmon. Preliminary analysis of the pink salmon data suggested that individual fish might be an important factor explaining variation in swimming and ground speeds as well as energy use. A reanalysis was conducted of Hinch and Rand's (1998) data because they did not consider "individual fish" as a factor responsible for variation.

Daily average water temperatures (measured by Fisheries and Oceans Canada at Hell's Gate, situated approximately 10 km upstream of the study area) were 13.9–15.4 and 14.0–17.0°C during the field seasons in 1999 and 1993, respectively. Daily average discharge (measured by Water Survey of Canada at Hope, B.C., approximately 20 km downstream of the study area) ranged from 1900 to 4030 (mean 2758) and 3170 to 3770 (mean 3295) m^3·s^{-1} for 1999 and 1993, respectively.

Statistical analyses

Analysis of covariance (ANCOVA) was used to compare the slopes and intercepts of the linear relationships between TBF and EMGPI from the swimming tunnel trials to determine if separate predictive relationships were required for fish of specific sizes or sex. If error variance heteroscedasticity existed, TBF was log transformed prior to analysis. Differences in mass and length between the sexes of fish used in the swimming tunnel were determined by analysis of variance (ANOVA). To assess differences in condition between the sexes, sex-specific log mass versus length regression relationships were compared with ANCOVA.

To examine the speeds and energy use of upriver migrating pink salmon, three separate split-plot repeated-measures ANOVAs were used and then type III sums of squares were interpreted (SAS 1988). Separate analyses were performed using ground speed (cm·s^{-1}), swimming speed (cm·s^{-1}), and energy use (J·m^{-1}) as dependent variables. In each analysis, sex was the treatment (two sexes = 1 degree of freedom (df)), river reach (nine reaches = 8 df) was the repeated measure with individual fish as replicates (six fish, two sexes = 10 df). Within this model, sex was tested using the fish nested in sex error term (10 df), and all other dependent variables were tested using the full model error ((reach* fish(sex)) = 80 df, which may vary due to missing values). All models were tested for interaction between sex and reach. If an interaction was detected, further two-way ANOVAs with sex and reach as main effects were conducted to isolate the interactive terms. Differences among individuals, sexes, and reaches were determined a posteriori using least square

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means (LSM). Pearson's correlation between weight and swimming speed, ground speed, and energy use were also examined to speculate on the role that fish size might have on the response variables. Differences in weight between fish were determined using two-way ANOVA and a least significant difference t test.

We combined our data with that used by Hinch and Rand (1998) to compare energy use of sockeye and pink salmon. Species and sex classes were combined into one main effect variable that was termed species–sex class that had four levels (sockeye females, sockeye males, pink females, and pink males, four classes = 3 df). Because a sex by species interaction could not be tested for in these analyses, two additional split-plot repeated-measures ANOVAs were conducted with sex and then species replacing sex–year class as main effects. One-way ANOVAs were used to compare fish body mass among the sex and species groups. LSM were used as the a posteriori approach for assessing differences among levels within the class variables. Following each ANOVA, plots of residual versus predicted values were examined to look for error variance heteroscedasticity. If present, log transformations were applied and the ANOVAs redone. The coefficient of variation (CV) of energy use was calculated for each species–sex class. Two-way ANOVAs were then used to compare CV values among sex–species and reach. Statistical significance was assessed at the 0.05 level. Significance levels for all a posteriori contrasts were adjusted using Bonferroni's method. All analyses were conducted using SAS (1988).

Results

Swimming tunnel study

There were no differences in mean length or mean mass between sexes for the pink salmon ($P = 0.9642$ and 0.4583, respectively; overall mean length 52.0 cm, overall mean mass 1.6 kg). Furthermore, neither the slopes nor intercepts of the log mass versus length regression relationships differed between sexes ($P = 0.4991$ and 0.5690, respectively). The TBF versus EMGPI regression slopes differed among individuals ($P = 0.0001$). These differences were primarily due to sex. When separate ANCOVAs for males and females were conducted, the slopes of the male fish did not differ ($P = 0.3147$), nor did those of the female fish ($P = 0.2081$). Therefore, common regression relationships were developed for males and females by pooling data within sexes (Fig. 2). Hinch and Rand (1998) found that fish size was also an important independent variable helping to predict TBF in sockeye salmon. We found with multiple regression that mass significantly contributed to explaining variation in TBF (for both sexes, $P < 0.0001$). Thus, the regression models used for predicting TBF from EMGPI are log TBF = –0.0004186EMGPI + 0.1731621mass + 0.5796416 for males (Fig. 2*a*; $P < 0.0001$, $r^2 = 0.84$, SE intercept = 0.036, SE mass = 0.016, SE EMGPI = 0.00002) and log TBF = –0.0003026EMGPI – 0.1646546mass + 0.9171931 for females (Fig. 2*b*; $P < 0.0001$, $r^2 = 0.53$, SE intercept = 0.022, SE mass = 0.012, SE EMGPI = 0.000009). EMGPI values ranged from 1950 to 500 ms, which corresponded to predicted TBF values of 1.10 to 4.44 beats·s^{-1} for an average-sized fish (1.6 kg). Estimates of instantaneous swimming speeds associated with those TBF values ranged from 63.03 to 209.62 cm·s^{-1}. For females, the EMGPI values ranged from 1800 to 550 ms, which corresponded to predicted TBF values of 1.29 to 3.07 beats·s^{-1} for an average-sized fish. Estimates of instantaneous swimming speeds associated with those TBF values ranged from 71.28 to 149.59 cm·s^{-1}.

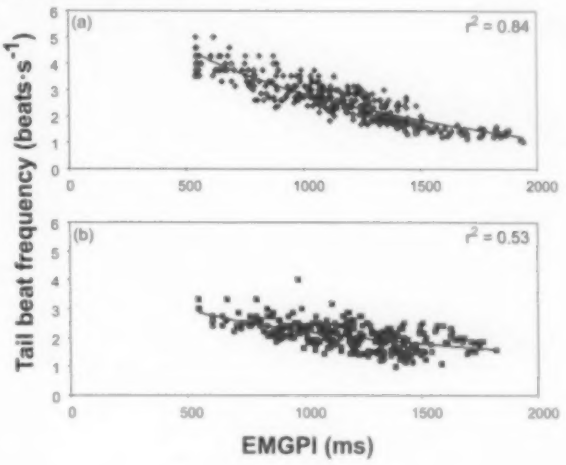

Fig. 2. Relationships between electromyogram pulse interval (EMGPI; in milliseconds (ms)) and tail beat frequency (beats·s^{-1}) for (*a*) male ($n = 4$) and (*b*) female ($n = 4$) pink salmon (*Oncorhynchus gorbuscha*) developed using a swimming tunnel. Exponential regression line and coefficients of determination are presented for each sex.

Telemetry study

Pink salmon

Male pink salmon (mean mass 1.79 kg) used in the telemetry study were larger than the female pink salmon (mean mass 1.18 kg, $P = 0.0090$). However, there were no differences between mass of males used in calibration study and those used in telemetry study, nor between mass of females used in calibration study and those used in telemetry study ($P > 0.05$ for both).

The split-plot repeated-measures ANOVA revealed that swimming speeds varied among individual fish ($F_{[10,66]} = 77.48$, $P = 0.0001$) and among reaches ($F_{[8,66]} = 10.38$, $P = 0.0001$) but did not vary between sexes ($F_{[1,10]} = 0.00$, $P = 0.9625$). Swimming speeds of pink salmon ranged from 51 to 183 cm·s^{-1} (mean 114 cm·s^{-1}, $n = 93$, SE = 2.9) among fish and reaches. Swimming speeds were fastest through reaches 4 and 6 and slowest through reach 8 (Table 1).

Pink salmon ground speed data required log transformation. The split-plot repeated-measures ANOVA revealed no differences among individual fish ($F_{[10,64]} = 1.27$, $P = 0.2643$) or between sexes ($F_{[1,10]} = 0.09$, $P = 0.7758$) in pink salmon ground speeds; however, differences were evident among river reaches ($F_{[8,64]} = 6.80$, $P = 0.0001$). Average ground speeds varied from 21.2 to 114.3 cm·s^{-1} (mean = 57.1, $n = 9$, SE = 11.13) among reaches. Among reaches, ground speeds fell into two general groups: fast (reaches 1 and 5) and slow (reaches 3, 4, 7, 8, and 9) (Table 1).

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Table 1. Means and standard errors (SE) of swimming speeds, ground speeds and energy use of pink salmon migrating through the nine reaches.

	Reach								
	1	2	3	4	5	6	7	8	9
Bank morphology class	Bend	Straight	Bend	Constricted	Bend	Bend	Constricted	Straight	Constricted
Mean centre-line current speed ($cm \cdot s^{-1}$)	46	147	147	385	50	500	—	357	292
Mean swimming speed ($cm \cdot s^{-1}$)	107.11	116.93	117.08	123.55	95.79	127	110.76	91.82	107.09
SE swimming speed ($cm \cdot s^{-1}$)	6.41	5.66	5.66	5.99	5.98	5.66	5.99	6.71	11.23
Bonferroni contrasts of swimming speed	A B C	B C	B C	C	A B	C	A B C	A	A B C
Mean ground speed ($cm \cdot s^{-1}$)	93.77	88.55	34	43.63	112.13	56.98	30	43.29	25.36
SE ground speed ($cm \cdot s^{-1}$)	17.53	14.82	14.82	15.69	15.65	15.65	15.69	17.58	29.58
Bonferroni contrasts of ground speed	C	B C	A B	A B	C	B C	A	A B	A
Mean energy use ($J \cdot m^{-1}$)	0.18	0.23	0.29	0.38	0.6	0.24	0.32	0.11	0.63
SE energy use ($J \cdot m^{-1}$)	0.07	0.06	0.06	0.06	0.06	0.06	0.06	0.07	0.12
Bonferroni contrasts of energy use	A	B C	C D	C D	A	B C D	D	B C	C D

Note: Sexes were pooled for these calculations. Means and SE are based on raw nontransformed data. Fish sample sizes are presented on Fig. 3. Bonferroni contrasts are based on analysis of variance (ANOVA) results, which examined log-transformed ground speeds and energy use. Reaches with similar letters are not different. Bank classes and mean centre-line current speeds are given for each reach. Current speeds could not be obtained at reach 7 because of dangerous access and flow conditions.

Pink salmon energy-use data required log transformation. The split-plot repeated-measures ANOVA revealed that variation in energy use was attributed to differences among individual fish ($F_{[10,64]} = 11.29$, $P = 0.0001$) and among reaches ($F_{[8,64]} = 8.36$, $P = 0.0001$) but not between sexes ($F_{[1,10]} = 0.75$, $P = 0.4058$). Average energy use varied from 0.002 to 1.73 $J \cdot m^{-1}$ (mean = 0.26, $n = 92$, SE = 0.032) among reaches and individuals. Energy use fell into two general reach groupings: low (reaches 1 and 5) and high (reaches 3, 4, 6, 7, and 9) (Table 1).

Contrasting pink and sockeye salmon

Male sockeye salmon (mean mass 2.64 kg) were larger than female sockeye salmon (mean mass 1.75 kg, $P < 0.0001$). In contrasting sex–species classes, only pink males and sockeye females were not different in mass ($P > 0.05$). The repeated-measures ANOVA examining the combined data sets for pink and sockeye salmon swimming speeds revealed significant differences between individual fish ($F_{[17,111]} = 6.53$, $P = 0.0001$), reach ($F_{[8,111]} = 6.53$, $P = 0.0001$), and an interaction between reach and species–sex class ($F_{[24,111]} = 2.18$, $P = 0.0035$). The main effect of species–sex class was not significant ($F_{[3,17]} = 0.57$, $P = 0.6392$). We reduced the number of reaches in our a posteriori contrasts to more easily interpret the interaction term. We took this approach because the Bonferroni adjustment of $\alpha = 0.05/16$ is a highly conservative interpretive tool and resulted in no significant differences being detected in any comparisons, despite the ANOVA revealing a significant interaction term. Reaches 2, 4, 7, and 9 were scrutinized because they represented the full, among-reach range of hydraulic conditions in this study (Table 1). Pink females (PF) swam faster than sockeye females (SF) in reaches 4 (PF mean = 121 $cm \cdot s^{-1}$, SF mean = 97 $cm \cdot s^{-1}$, $P = 0.0613$), 2 (PF mean = 117 $cm \cdot s^{-1}$, SF mean = 78 $cm \cdot s^{-1}$, $P = 0.0181$), and 9 (PF mean = 95 $cm \cdot s^{-1}$, SF mean = 63 $cm \cdot s^{-1}$, $P = 0.0060$) but not in reach 7 ($P = 0.5211$). Pink females swam faster than sockeye males (SM) in reach 2 (PF mean = 117 $cm \cdot s^{-1}$, SM mean = 91 $cm \cdot s^{-1}$, $P = 0.0608$) but not in the other reaches (all $P \geq 0.26$). Pink males (PM) swam faster than sockeye males in reach 2 (PM mean = 117 $cm \cdot s^{-1}$, SM mean = 91 $cm \cdot s^{-1}$, $P = 0.0576$) but not in reaches 4, 7, and 9 ($P \geq 0.2885$). Pink males also used less energy than sockeye females in reach 2 (PM mean = 117 $cm \cdot s^{-1}$, SF mean = 78 $cm \cdot s^{-1}$, $P = 0.0170$), 4 (PM mean = 125 $cm \cdot s^{-1}$, SF mean = 97 $cm \cdot s^{-1}$, $P = 0.0254$), and 9 (PM mean = 138 $cm \cdot s^{-1}$, SF mean = 63 $cm \cdot s^{-1}$, $P = 0.0076$) but not in reach 7 ($P = 0.5040$).

Ground speed data for all species–sex classes required log transformation. For ground speed, species–sex class ($F_{[3,17]} = 3.45$, $P = 0.0402$) and reach ($F_{[8,109]} = 9.67$, $P \leq 0.0001$) were significant. Individual fish was not a significant variable ($F_{[17,109]} = 0.82$, $P = 0.6642$) and there was no interaction between species–sex class and reach ($F_{[24,109]} = 0.85$, $P = 0.6702$). Both pink females (mean = 54.2 $cm \cdot s^{-1}$, $n = 46$, SE = 6.3, $P = 0.0003$) and pink males (mean = 63.4 $cm \cdot s^{-1}$, $n = 46$, SE = 10.1, $P = 0.0017$) migrated faster than sockeye females (mean = 33.9 $cm \cdot s^{-1}$, $n = 34$, SE = 3.8). All sex–species classes had slower ground speeds through reaches 4 (mean = 31.6 $cm \cdot s^{-1}$, $n = 20$, SE = 4.9), 7 (mean = 28.5 $cm \cdot s^{-1}$, $n = 18$, SE = 4.3), and 9 (mean = 24.0 $cm \cdot s^{-1}$, $n = 12$, SE = 3.6) than through reach 2 (mean = 77.6 $cm \cdot s^{-1}$, $n = 20$, SE = 19.1).

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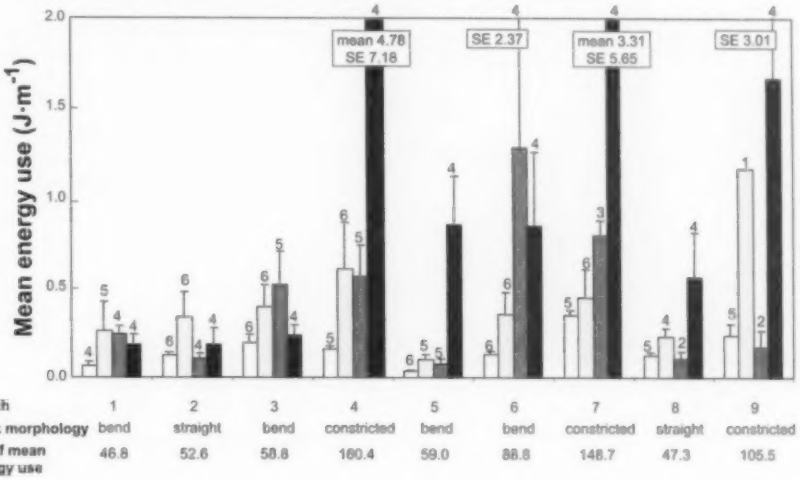
Fig. 3. Mean energy use (+1 SE) in each reach for pink salmon (*Oncorhynchus gorbuscha*) females (open bars) and males (light shading) and for sockeye salmon (*Oncorhynchus nerka*) females (dark shading) and males (solid bars). The first row of digits under the horizontal axis indicates the reach number. The second row is the coefficient of variation (CV) of energy use based on the four species–sex mean energy-use values. Numbers above each bar are sample sizes. In some instances, means and upper standard error (SE) values extend off the figure, these out-of-range values are indicated.



Energy-use data for all species–sex classes required log transformation. Energy use varied among individuals ($F_{[17,109]} = 9.44$, $P \leq 0.0001$) and there was interaction between species–sex class and reach ($F_{[24,109]} = 2.01$, $P = 0.0082$; Fig. 3). Again we used the reduced data set to interpret the interaction as outlined above for the swimming speed data. In reach 4, pink females and pink males used less energy than sockeye males ($P < 0.001$ for both; Fig. 3). Averaging among sex–species classes, reaches 4 and 7 had higher energy use than reach 2 ($P \leq 0.0001$ for both contrasts; Fig. 3). When sex–species class was replaced with sex as a main effect in the same ANOVA, energy use varied among reaches ($P = 0.0001$) but not between sexes ($P = 0.3294$). Likewise when species was used as the main effect, energy use varied strongly among reaches ($P = 0.0001$) but not between species ($P = 0.0986$).

Within-group variation in swimming speed differed among sex–species classes ($F_{[3,23]} = 22.26$, $P = 0.0001$; Fig. 3). Swimming speeds for pink salmon females (mean CV = 13.2) were less variable than those for pink salmon males (mean CV = 36.6; LSM, $P = 0.0005$). Sockeye salmon females (mean CV = 22.6) did not differ in swimming speed variation from pink salmon females (LSM, $P = 0.0972$) or pink salmon males (LSM, $P = 0.0275$). Swimming speeds for sockeye salmon males (mean CV = 55.0) were more variable than those for female pink salmon ($P = 0.0001$), male pink salmon ($P = 0.0001$), and female sockeye salmon (LSM, $P \leq 0.0001$). Within-group variation in log ground speed ($F_{[3,23]} = 0.75$, $P = 0.5361$) or log energy use ($F_{[3,23]} = 0.99$, $P = 0.4168$) did not differ among sex–species classes. Within species–sex group variation in swimming speed ($F_{[8,23]} = 0.42$, $P = 0.8987$), log energy use ($F_{[8,23]} = 0.99$, $P = 0.4666$), and log ground speed ($F_{[8,23]} = 1.54$, $P = 0.1964$) did not differ between reaches (Fig. 3). As a summary of energy-use variability among reaches, CV was calculated based on the four species–sex mean energy-use values at each reach (presented in Fig. 3).

Discussion

As we found in our reanalyses of their data, Hinch and Rand (1998) found that reaches with constrictions were the most energetically costly for migration of sockeye salmon. We also found this for pink salmon, although it is somewhat more complicated. Certainly constricted reaches (e.g., 4, 7, and 9) caused high energy use for pink salmon, but so did reaches 3 and 6. The latter had large bends and relatively fast surface currents (unlike the other reaches with bends that had relatively slow currents). The common feature among these five reaches is that the combination of their bank morphologies and current speeds would result in extremely complex surface and subsurface flow patterns. Energy use is accelerated by increased swimming speeds or increased ground speeds, and our results indicate that depending on the reach, either one or both are responsible for high energy-use values. Flow complexity can cause an increase to both swimming speeds and ground speeds. Hinch and Rand (2000) used underwater video to examine swimming speed, encountered water velocities, and ground speeds of upriver-migrating sockeye salmon and found that at nonturbulent and slow water sites, fish adjusted their swimming speeds to achieve ground speeds that resulted in energetically minimal costs. However, when encountered currents were relatively fast and turbulent, fish chose to swim relatively fast and not elicit this energy-saving behaviour. They speculated that at fast, turbulent sites, salmon might be attempting to minimize their travel times because they only have a short while to live and significant migration impediments could seriously affect arrival times on spawning grounds and hence negatively affect spawning success.

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It is equally likely that complex, turbulent, and fast currents prevent fish from readily locating migration cues thus taking longer to find a desired path and therefore having decreased ground speeds. The diminished ability to locate cues and paths is supported by the among-reach variability (as measured by the CV) in energy use that we found. Reaches with complex flow patterns probably have the greatest diversity of hydraulic conditions, allowing for a greater number of possible migratory routes, which could explain the relatively higher among-individual variation in energy use that we found at these complex flow reaches. A closer examination of migration path choice suggests that migrating fish cross the river and backtrack more often at reaches with constrictions (Standen 2001; Hinch et al. 2002). This may be evidence that the fish are being diverted by strong, turbulent flows or that they are attempting to locate small-scale low velocity fields for upriver migration. Whichever the reason, small-scale hydraulic conditions appear to be of great importance in determining behaviour and resultant energy use in migrating salmon. In sum, whether caused by a desire to reduce travel time thereby elevating swimming speed or by an inability to locate appropriate paths thereby decreasing ground speed, river reaches with constrictions and those where currents are fast and deflected by river bends cause pink and sockeye salmon to use relatively high levels of energy during migration.

Hinch and Rand (1998) found that during migration, male sockeye used more energy than female sockeye. The present reanalysis of their data suggests that this depends upon reach. Male sockeye exhibited the most costly migrations at constricted reaches (e.g., reaches 4, 7, and 9). Our present results differ from those of Hinch and Rand (1998) for two reasons. First, to analyze their data, they chose to use a two-way ANOVA that did not take individual variation into consideration, unlike the repeated-measures split plot used in this analysis. Large individual variation may be masking stronger differences between sexes. Of equal importance, this analysis used only a subsample of their sites. They included three very low velocity sites on the Nechako River as well as the much more constricted Hell's Gate site on the Fraser River. Hinch and Rand found strong differences between sexes at Hell's Gate, which supports the findings of this study that differences between the sexes become more apparent in areas of difficult passage.

In pink salmon, we found no statistically significant differences in energy use between males and females. Although not statistically different, male energy use at each reach was always higher than that of females, and as with sockeye, differences were most evident at our constricted, fast-flowing reaches (reaches 4 and 9) where males used over 4 times the energy of females. Based on swimming tunnel experiments, Williams and Brett (1987) estimated that male pink salmon use 15% more energy than females to swim the same distance. Thus it is likely that sex differences exist but our sample size may have been too low for adequate detection.

Several factors can explain why adult male salmon seem to use more energy than adult females during migration through reaches with fast and complex flows. Increased selective pressure for migration efficiency likely exists for females because they must allocate relatively more energy to egg production than males do for milt production (Gilhousen 1980; Jonsson et al. 1991; Brett 1995). Also males undergo a much more distinct morphological change. Males develop a large dorsal hump and extended kype (Brett 1995). This change in shape may increase their hydrodynamic drag (Weihs and Webb 1983; Videler 1993) and potentially force them to increase their swimming speed and energy expenditure to reach the spawning grounds at the same time as females. A difference between sexes in hydrodynamic drag may be most evident at reaches with fast and complex flows. There may also be increased physiological differences in the cardiac and metabolic processes between males and females as they near reproductive maturity. During respirometer trials with sockeye salmon, males swam at consistently higher $V_{O_2\,max}$ (the maximum volume of oxygen consumed by a swimming fish) than females of the same size, indicating that females are more efficient swimmers (Christopher G. Lee, Biology Department, Simon Fraser University, Burnaby, B.C., unpublished data). Webb's (1995) theory that fish can minimize energy use by swimming at metabolic and hydrodynamic optimal speeds suggests that differences in physical shape and metabolism between the sexes could cause them to have different energy-use minima.

Contrary to our original prediction, pink salmon were not less efficient (used less energy per metre) than sockeye salmon. There were no statistical differences between the species, and there was a trend towards pink salmon actually being more efficient. This was most noticeable at the reaches with fast water speeds (e.g., reaches 4 and 6). Interspecific differences in migration paths probably exist and these may be responsible for any differences in energy use between species. Using a split-beam echosounder, Xie et al. (1997) found that pink salmon migrated in tight groups close to shore near the bottom of the river, whereas sockeye migrated in less dense aggregates further from shore and throughout the water column. River velocities generally increase with distance away from the bank and bed of the river (Henderson 1966), which would suggest that sockeye are encountering faster currents that could be more costly to migrate. As well, Seton River pink salmon migrate only one-third the distance of the Early Stuart sockeye salmon. Because of the longer migration distance they travel to reach their spawning grounds and the small temporal window they have in which to do it, Early Stuart sockeye salmon may be swimming at faster, more energy-demanding speeds.

Two assumptions were made to compare the migration energetics of pink and sockeye salmon. First, although pink and sockeye salmon were studied through the same reaches in the Fraser River, they were studied in different years. However, temperature and river discharge were very similar during the periods of study of the two species, particularly when one considers how variable these features can be interannually (Macdonald 2000). Second, a sockeye salmon bioenergetics model (Hinch and Rand 1998) was used to predict energy use for pink salmon. Currently a bioenergetics model for pink salmon does not exist. Williams and Brett (1987) determined that the U_{crit} (the swimming velocity at which a fish can sustain itself for 60 min before reaching exhaustion and failing to swim) for pink salmon was similar to that for sockeye, suggesting that bioenergetics parameters may be similar between species, yet Brett (1982) found that pink salmon required higher amounts of energy to maintain U_{crit}

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swimming. These types of conflicting results may reflect the fact that different stocks of pink salmon were used in those two studies. Studies of swimming metabolism on Seton pink salmon and Early Stuart sockeye salmon are needed to better understand their endogenous swimming abilities. Lastly, although not an assumption, sample size was a general limitation to this study. The lack of strong differences between sexes and species may be due to small sample size and resulting large individual variation within each species–sex group.

Our interpretations of EMG data from migrating fish are determined by our laboratory EMG – swimming speed relationships. Other laboratory swimming tunnel studies in which EMG technology has been used to assess swimming speeds of salmonids have found that individual fish can vary in their EMG – swimming speed relationships, resulting from size, sex, and transmitter-specific factors (reviewed in Thorstad et al. 2000). Within this study we have minimized these potential differences by including size and sex as covariates in the models. In terms of transmitter-specific factors, EMG information can vary with the muscle insertion position of the sensing electrodes and with subtle technical differences among transmitter electronics. We implanted electrodes using methods and insertion positions that were identical for each fish, although there may have been minor differences among fish. We have no control over factory-generated differences in transmitter electronics. However, there is no reason to suspect that these transmitter factors have caused a bias in our interpretations. In other words, they should not affect one sex, species, or reach more than another. Transmitter factors should contribute to the levels of unexplained variation that we report in individual-specific EMG data. The fact that we can detect consistent and strong differences among reaches in EMG patterns indicates just how influential this variable is in the face of these other potential sources of variation. Ideally, one should develop EMG – swimming speed calibration relationships for each individual fish (and transmitter) that is being tracked in the wild (e.g., first swim the fish in vivo before studying it in situ) (e.g., Geist et al. 2002). We have found that this is not possible with mature Pacific salmon that are very near death; fish do not seem able to fully recover from laboratory performance experiments and successfully complete their migration. Although previous work on Columbia River spring chinook salmon (*Oncorhynchus tshawytscha*) showed that these fish were able to be calibrated and successfully released, recent work on upriver-migrating fall chinook salmon (Brown and Geist 2002), which were closer to death than spring chinook at the time of their study, were less likely to survive the calibration process (D.R. Geist, Pacific Northwest National Laboratory, P.O. Box 999, MSIN: K6-85, Richland, WA 99352, U.S.A., personal communication).

Our estimates of actual energy expenditure are likely an underestimate of the true costs because the bioenergetics model only includes costs attributable to aerobic metabolism. It is clear that anaerobic metabolism occurs in sockeye salmon at our sites (Rand and Hinch 1998) and likely also in pink salmon (Hinch et al. 2002). Using the same EMG data summarized in the present study, Hinch et al. (2002) calculated that 5–10% of the time, burst speeds (which are fueled by anaerobic metabolism) were being elicited by both species in our reaches. The higher percentage values were at the reaches with constrictions, indicating that these reaches are more energetically costly than our present results suggest. Furthermore, if figured into total energetic costs, these additional anaerobic costs could thus make the migrations of pink salmon males more expensive than those of pink salmon females, thereby strengthening our original prediction that male salmon are less energetically efficient at migration than females.

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PERSPECTIVE

Changing times, spaces, and faces: tests and implications of adaptive morphological plasticity in the fishes of northern postglacial lakes

Beren W. Robinson and Kevin J. Parsons

Abstract: The phenotypic diversity exhibited within and among populations of freshwater fishes in postglacial lakes has intrigued biologists for two reasons: (*i*) their high phenotypic variation and (*ii*) the apparently recent and rapid divergence of forms. Genetic and ecological studies of these taxa are shedding new light on mechanisms of divergence and species formation. Surprisingly, the roles of phenotypic plasticity in the origins, maintenance, and generation of phenotypic diversity in this system are rarely directly addressed. We synthesize the available literature on morphological plasticity in these fishes and, using a meta-analysis, test for adaptive plasticity. We conclude that (*i*) morphological plasticity is common in at least six families of northern freshwater fishes, (*ii*) plastic responses can often be induced by conditions related to littoral and pelagic lake environments, (*iii*) plasticity often represents adaptive responses to conditions in these habitats, and (*iv*) that although rarely tested, heritable variation in morphological plasticity is present. The rich amount of phenotypic plasticity has not constrained recent adaptive divergence and species formation in postglacial fishes, and instead plasticity may play a role in the notably high rates of divergence observed in these and other fishes currently undergoing adaptive radiation.

Résumé : La diversité phénotypique qui se manifeste au sein des populations et entre les populations de poissons d'eau douce dans les lacs postglaciaires intrigue les biologistes pour deux raisons, soit (*i*) l'importance de la variation phénotypique et (*ii*) la divergence apparemment récente et rapide des formes. Les études génétiques et écologiques de ces taxons (*ii*) apportent de nouvelles perspectives sur les mécanismes de divergence et de formation d'espèces. Curieusement, le rôle de la plasticité phénotypique dans l'origine, le maintien et la production de la diversité phénotypique n'est que rarement abordé directement. On trouvera ici une synthèse de la littérature sur la plasticité morphologique de ces poissons ainsi qu'un test de plasticité adaptative basé sur une méta-analyse. Nos conclusions sont que (*i*) la plasticité morphologique est répandue chez au moins six familles de poissons nordiques, (*ii*) les réactions impliquant la plasticité peuvent souvent être induites par des conditions propres aux environnements littoraux et pélagiques des lacs, (*iii*) la plasticité représente souvent une réaction adaptative aux conditions dans ces habitats et (*iv*) il existe une variation héréditaire de cette plasticité, même si elle a été rarement testée. L'importance considérable de plasticité phénotypique n'a pas restreint la divergence adaptative récente ni la formation d'espèces chez ces poissons postglaciaires; au contraire, la plasticité peut sans doute expliquer en partie les taux remarquablement élevés de divergence observés chez ces poissons et chez d'autres qui subissent actuellement une radiation adaptative.

[Traduit par la Rédaction]

Introduction

Phenotypic variation observed within and among natural populations arises from two proximate and interacting mechanisms: genetic differences among forms and environmentally induced modifications of the phenotype during development, referred to as phenotypic plasticity (Scheiner 1993). The type and degree of environmentally induced differences are referred to as a genotype's reaction norm. Northern freshwater fishes that inhabit postglacial environments show remarkable amounts of phenotypic variability but unusually low amounts of genetic diversity among forms (Bernatchez and Wilson 1998). This has led some to conclude that these fishes exhibit unusually high levels of morphological plasticity. A consequence of inferring plasticity in this way is that it leaves the impression that such plasticity is neither ecologically nor evolutionarily relevant to understanding the sources and maintenance of diversity in this system. The available literature shows that only two taxa have been directly tested for adaptive plasticity in morphology (the crucian carp (*Carassius carassius*) and the threespine stickleback (*Gasterosteus aculeatus*)). No direct tests have been performed using salmonids or whitefish, the taxa typically found at the

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center of long-standing debates about the importance of variation in northern freshwater fishes. This suggests a biased perspective that views morphological plasticity as an unimportant phenomenon.

Our purpose is to review and meta-analyze studies of morphological plasticity in the fishes of postglacial environments with the goal of testing the general hypothesis that much of the observed morphological plasticity is not adaptive. We predict that morphological plasticity can often be adaptive in postglacial lake environments and that it has evolved to maximize fitness under environmental variation. Throughout, we also discuss how plasticity can influence the outcome of species interactions and habitat use and the rate and direction of evolutionary divergence in these fishes.

Phenotypic variation in northern freshwater fishes

The phenotypic variation of northern freshwater fishes has challenged biologists for more than a century, as demonstrated by historic species names such as "*inconstans*", "*perplexus*", "*variabile*", and "*variabilis*". The problem is in the identification of biological units that can be used for taxonomic or stock management purposes. A primary goal has been to develop a relatively consistent and appropriate assignment of forms to stocks, species, genera, or other units. The difficulty of this task is reflected in at least 100 years of research on the "char problem", an attempt to classify the phenotypic variation within and among populations of Arctic char (*Salvelinus alpinus*; Nordeng 1983; Behnke 1989; Nyman 1989). Whitefish (subfamily Coregonines) is another case in which even supposedly stable features, such as gill raker number (a common stock identification trait), can rapidly change. Lindsey (1981) viewed some whitefish stocks as chameleons, able to rapidly shift their number of gill rakers in response to other fish competitors. Systematists have also been bewildered by the diversity of freshwater threespine sticklebacks (*Gasterosteus*); at one point, at least 40 different "species" were identified (Bell and Foster 1994). This system was taxonomically simplified to a single variable species providing rich opportunities to study adaptive divergence, species formation, and radiation. Similar classification problems occur for anadromous and freshwater forms of other northern taxa (Bell and Andrews 1998).

Two features are noteworthy in all of these cases. First, similar patterns of phenotypic variation exist in a hierarchy, including variation among forms that coexist in single populations (Robinson and Wilson 1994; Smith and Skulason 1996; Robinson and Schluter 2000), variation among populations of a single species that can exist across hundreds of isolated lakes or river systems (Behnke 1989; Robinson and Wilson 1994), and variation among coexisting closely related species (Lindsey 1981; Smith and Todd 1984; Schluter 1996). This suggests that phenotypic variation found within species can sometimes be rapidly converted into variation between species (Smith and Skulason 1996; Robinson and Schluter 2000).

Second, where such variation occurs in lakes, it is often predictably repeatedly in association with particular environments (Robinson and Wilson 1994; Smith and Skulason 1996; Robinson and Schluter 2000). Strong or persistent associations between phenotype and resource use are a hallmark of adaptation (Schluter 2000). Divergent forms are often found in the littoral or pelagic environments (sometimes identified, respectively, as benthic or limnetic habitats) of many postglacial lakes in North America and Eurasia. The repeated divergence into littoral and pelagic habitats also suggests that these environmental niches are common features of many postglacial lakes (Robinson and Wilson 1994). These habitats are expected to be ecologically distinct in many lakes because they differ with respect to many abiotic and biotic conditions (such as light, temperature, structure, oxygen level, pH, prey taxa, prey size, prey hardness, and the presence of competitors and predators; Smith and Todd 1984; Horne and Goldman 1994; Schindler and Scheuerell 2002). These differences are expected to impose divergent selection that favors different phenotypes in each environment (Smith and Todd 1984; Behnke 1989; Smith and Skulason 1996). This prediction has gained support from direct tests of habitat-specific performance of phenotypes (Schluter 1995; Robinson 2000; Proulx and Magnan 2002).

Phenotypic plasticity in northern freshwater fishes

Postglacial fishes also exhibit considerable plasticity in behavioral, life history, and physiological characters. Research on the behavioral plasticity of fishes is well advanced and has focused on the lability of behaviour related to foraging, habitat use, and predator avoidance (e.g., Dill 1983; Tulley and Huntingford 1987; Grand and Dill 1996). We do not focus on behavioral plasticity except to note that it can be related to plasticity in morphology (e.g., Day and McPhail 1996) and life history (Metcalfe 1993).

Fish taxa are also being studied with respect to life history plasticity. Numerous taxa are plastic with respect to growth, age and size at maturity, and the allocation of resources to reproductive vs. somatic tissue (e.g., Stearns and Koella 1986; Gross 1996; Hutchings 1996). We exclude life history plasticity from our analysis except where it is related to morphological plasticity. This simplifies our task of synthesizing the literature and allows us to ignore some additional complexities in life history plasticity. Changes in growth rate and body size resulting from resource abundance often influence life history in fishes (Hutchings 1996). However, diet and life history are not as consistently linked to body size in fishes as they are in mammals. For example "dwarf" populations of whitefish and char in certain areas inhabit littoral habitats, and elsewhere pelagic habitats (e.g., Behnke 1989; Bernatchez and Dodson 1990). To our knowledge, the only consistent cross-taxon relationships between body size and habitat or trophic niche occurs with respect to piscivory and to the onset of migration in anadromous fishes.

Ontogenetic niche shifts also suggest a link between ecology and body size, but consistent relationships between body size, diet, and habitat use generally occur within and not among fish species. This indicates to us that these relationships have been modified by other taxon specific factors. For example, sunfish fry are zooplanktivorous, returning to the natal littoral habitat as juveniles where they feed on larger invertebrate prey (Osenberg et al. 1988). They either remain there as adults (e.g., pumpkinseed sunfish, *Lepomis gibbosus*) or return to planktivory in the pelagic zone (e.g., bluegill sunfish, *Lepomis macrochirrus*). A reverse ordering can occur in char that are benthivorous as young-of-year and juveniles, shift to feeding on zooplankton in the water column with in-

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creasing size, followed sometimes by piscivory at the largest sizes (e.g., Klemetsen and Dahl-Hansen 1995). These examples highlight the fact that the relationships between body size and foraging mode or habitat use in fish are rarely uniform because they integrate many other important ecological factors. Although poorly quantified, behavioral, life history, and morphological plasticity are strongly interrelated in some fishes, (e.g., Hindar and Jonsson 1993; Metcalfe 1993; Day and McPhail 1996). We cannot explore these complex relationships, however, until we have first explored the potential significance of morphological plasticity.

Morphological plasticity

Direct studies of morphological plasticity in fishes are still rare, except for tests of temperature-dependent development of meristic characters such as vertebrae, scale counts, and fin rays (e.g., Lindsey and Arnason 1981; Beacham 1990; Conover and Present 1990). The effects of temperature over a large latitudinal scale have been studied in fish with large distributions (e.g., Conover and Present 1990). We do not consider this here because we are primarily interested in morphological responses to environmental variation at the smaller scales within and among postglacial lakes. The effect of environment on inducible morphological responses at these smaller scales is not well understood. We also wish to consider continuously varying traits such as relative body depth, fin size and position, and relative head size, which along with other traits form the core of many contemporary ecomorphological studies in fishes (e.g., Norton et al. 1995).

Indirect evidence of morphological plasticity and divergent selection

Population genetic studies have shown that strikingly divergent forms of postglacial fishes exhibit little genetic divergence, indicating that morphological divergence can proceed more rapidly than neutral genetic divergence (Bernatchez and Wilson 1998; Schluter 2000). Two alternative explanations can account for this lack of correspondence: phenotypic differences are primarily due to environmentally induced effects (e.g., plastic responses), or neutral molecular genetic variation can be a poor indicator of early adaptive genetic divergence (e.g., Reed and Frankham 2001). This makes clear why the absence of molecular evidence of genetic divergence permits only weak inferences about phenotypic plasticity. Although neutral genetic divergence can sometimes be linked to adaptive genetic divergence, the absence of molecular divergence alone can be mute with respect to both adaptive divergence and phenotypic plasticity.

When genetic divergence is observed, the focus is on whether divergence is likely to have evolved by natural selection vs. random processes. Evidence strongly supports the divergence of forms during isolation in different glacial refugia (Bernatchez and Wilson 1998), although this does not discriminate between random processes and differential patterns of selection among glacial refugia. It does demonstrate an important historic component to the divergence of many fish taxa. Recent studies have also demonstrated that natural selection is currently driving the rapid divergence of numerous postglacial fishes at both interspecific and intraspecific levels (Schluter 2000). Schluter (1993, 1995) found evidence of divergent selection imposed on the morphology of "benthic" and "limnetic" species of the threespine stickleback. Trophic forms that coexist in single populations also seem to experience similar patterns of selection (Robinson and Wilson 1994; Smith and Skulason 1996; Robinson and Schluter 2000). Bernatchez and Wilson (1998) have also found that postglacial North American taxa have higher rates of genetic divergence and species formation than comparable nonpostglacial southern fish taxa. Adaptive plasticity is one evolutionary response to variable environmental conditions that imposes disruptive selection when suitable genetic variation in plasticity is available (Via and Lande 1985; Via et al. 1995). The relative indifference towards the potential for adaptive plasticity in northern freshwater fishes is curious in light of the role that divergent selection plays in postglacial lakes.

Methods to directly test for phenotypic plasticity

Four methods can be used to directly test for phenotypic plasticity in fishes. First, the progeny or a cohort of one (or more) form(s) is divided and reared under different controlled conditions in the lab or field (referred to below as a controlled reciprocal transplant (CRT) method). Lab conditions often involve different diets, prey, water velocity, or other specifically chosen conditions, whereas field conditions involve stocking enclosures located in specific habitats. Plasticity is demonstrated when phenotypic variation is induced in genetically similar individuals across different environmental conditions.

Second, the progeny of a form from a source lake is stocked into a transplant lake. Plasticity is demonstrated if the adult transplants are different from members of the source population (referred to here as an uncontrolled lake transplant (ULT) method). This comparison should not involve multiple generations in the transplant lake, as rapid genetic divergence between the two populations cannot then be ruled out. This method is "uncontrolled" in the sense that plastic responses cannot be definitively linked to specific environmental conditions.

Third, the progeny or a cohort from a wild-type form is reared in the lab or a hatchery and compared with its wild-type parents (uncontrolled artificial transplant (UAT) method). This is similar to the second method in that plasticity is demonstrated when progeny differ from their parents and the method is again "uncontrolled" because causal links between treatments and responses cannot be clearly established.

Fourth, the progeny or cohorts of multiple "wild-type" forms are reared together in a common environment in the lab, a hatchery, or in a field enclosure (referred to as a common garden experiment (CG) method). Plasticity is demonstrated if the differences among common gardened forms are reduced or disappear relative to the differences observed between wild types of the same age. Note that the convergence of two phenotypes simply reared in a common environment cannot be used to quantify plasticity because the convergence may to some degree be due to normal development (regardless of environment) rather than to induced responses to rearing conditions (e.g., Proulx and Magnan 2002).

These four methods allow the estimation of population mean norms of phenotypic reaction because morphology is assessed among forms of the same age in at least two envi-

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Table 1. Summary of 36 cases organized by taxa using one or a combination of direct methods to test for morphological plasticity in northern freshwater fishes.

				Source population	
Family	Genera	Species	No. of cases	Lake	River
Centrarchidae (sunfishes)	1	4	10	9	1
Coregonines (whitefish)	1	8	8	7	1
Cyprinidae (minnows)	1	1	3	3*	0
Gasterostidae (sticklebacks)	1	2	4	4	0
Percidae (perches)	1	1	3	3	0
Salmonidae (salmon–trout)	3	7	8	5	3
Total	8	22	36	31	5

Note: Further details of the studies are found in Appendix A.
*Includes two cases involving pond populations.

ronments. They also share one important assumption and vary in their ability to relate induced changes to specific environmental factors. The basic assumption is that there are no phenotype-dependent patterns of mortality with respect to treatment environments. If mortality within an environment is related to phenotype, then this could result in apparent mean phenotypic differences among groups (e.g., Hindar and Jonsson 1993) that are not necessarily the result of environmentally induced phenotypic changes. The effects of biased mortality can be tested for in the CRT and CG methods (first and fourth above), but not in the ULT or UAT methods (two or three above). When all groups are under care (as in CRT and CG), mortality can be monitored and, if low, can be ruled out as causing differences in mean phenotypes. When mortality is high, it can be ruled out if it is homogeneous across phenotypes within environments. Alternatively, fish that die may be collected and compared against survivors within treatments to test for phenotype-specific patterns of mortality. It is difficult to rule out the effects of nonrandom mortality in the ULT or UAT methods because mortality in at least one of the comparison groups is not monitored. We assume that environment-specific mortality effects are negligible in our analysis of the plasticity literature below.

These four methods also vary with respect to whether a causal link can be made between the induced phenotypes and specific environmental factors. Causal links can only be made using the CRT method. Inferring a causal relationship in the ULT method, even when lakes differ strongly on some known ecological factor(s), is possible but unreliable because lakes may vary with respect to other unknown but important conditions. The UAT and CG methods rarely permit tests of a causal link between environment and response because fish are usually reared under unspecified or unmonitored artificial conditions (but see Swain et al. 1991).

Review of direct tests of morphological plasticity

We found 36 cases that use one (or a combination) of the direct methods described above (Table 1; note that some individual studies in Appendix A include multiple species, populations, or forms that represent multiple tests or "cases" of plasticity). Two features are of particular interest. First, these cases involve 23 species from six taxa of northern freshwater fishes: sunfish, whitefish, minnows, sticklebacks, perch, and salmonids. Although this is moderately good representation at the family level given so few studies, this represents a relatively small fraction of the total number of northern freshwater fishes. Additional tests are warranted in other taxa. Second, 31 of the 36 cases use populations from lakes compared with 5 from rivers (Table 1). We speculate that this bias reflects a belief that lake populations exhibit more phenotypic variation than populations from rivers.

Eighteen of the 36 cases included treatment conditions related to littoral and pelagic lake environments (Table 2, Appendix A). These include enclosures placed in lake environments (n = 4), lab studies involving pelagic vs. littoral like prey (n = 12), or transplants between lakes strongly differing in littoral and pelagic conditions (n = 2). These cases involve five of the six families in Table 1. Tests of plastic responses to littoral vs. pelagic factors are reasonably well replicated within and among families. We use these results in our comparative tests of adaptive plasticity below. The remaining 18 studies included a variety of known treatments unrelated to littoral or pelagic lake habitats, such as water velocity (n = 3), predation (n = 3), food abundance (n = 1), or unknown ecological conditions arising from uncontrolled lake transplant studies (n = 3), and studies of forms reared in a common environment (n = 8). All studies that we have found have demonstrated morphological plasticity.

Tests of adaptive morphological plasticity

We now address whether the morphological plasticity of northern fishes can confer fitness advantages (for adaptive morphological plasticity in animals, see Gotthard and Nylin 1995). We limit our analysis to testing the advantages of plasticity with respect to littoral vs. pelagic conditions. We test three predictions relating to our hypothesis of adaptive plasticity: (1) induced phenotypes confer fitness-related advantages in the induction environment; (2) induced morphological responses (norms of reaction) are in directions predicted to increase performance and fitness; and (3) similar inducible morphological responses are repeatedly observed across evolutionarily independent populations and taxa that are reared between the same set of environmental conditions.

Prediction 1. Induced phenotypes confer advantages in their induction environment

Only 4 of the 36 cases of morphological plasticity tested if the induced form provided advantages under induction conditions (Table 3), consistent with our impression that adaptive morphological plasticity in postglacial fishes has

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Table 2. Classification of tests of morphological plasticity in northern fishes by treatment conditions.

	Treatment conditions		
Family	Littoral–pelagic	Other known	Unknown
Sunfish	Lake enclosures (1) Prey size–hardness (7)		Common garden (1)
Whitefish	Lake transplants (1)		Common garden (4) Lake transplants (3)
Minnows		Predator cues (3)* Food abundance (1)*	
Sticklebacks	Prey size–hardness (4)*		
Perch	Lake enclosures (3) Lake transplants (1)		
Salmon	Prey size–hardness (1)	Water velocity (3)	Common garden (3)
Column total	18	7	11

Note: We identify three general treatment categories: those directly related to conditions in littoral and pelagic lake environments, known conditions not directly related to these lake habitats, and unknown or undescribed conditions. Numbers in parentheses indicate the number of cases performed by that method. Asterisk (*) refers to cases where the performances of induced phenotypes were directly tested.

received little formal attention. The tests involve two taxa: crucian carp in response to predation and threespine sticklebacks in response to diet. Plasticity in the carp system is not related to littoral or pelagic conditions, our major focus; however, this system is a noteworthy example of how to test for adaptive plasticity in fish.

North European populations of the zooplanktivorous crucian carp (*C. carassius*) vary in body depth. In a series of pond and laboratory studies, Bronmark and Miner (1992) demonstrated that exposure to northern pike (*Esox lucius*), a large ambush predator of the littoral habitat, induced a deeper body form in carp. This was the first potential example of a predator-induced defensive phenotype in vertebrates. Pike generally swallow their prey head first; therefore, prey girth relative to mouth gape is expected to limit capture success. Nilsson et al. (1995) tested this hypothesis and found that pike handling time was positively related to body depth of carp and that pike preferentially attacked shallow- rather than deep-bodied carp. Carp change body form in response to chemical cues released by a variety of piscivores fed a diet of fish rather than to cues of any single taxa (Bronmark and Pettersson 1994). An untested alternative hypothesis is that a deeper body profile improves fast start in carp (Webb 1984*a*), providing a greater chance of escape during attack.

Adaptive plasticity is expected to evolve in response to variable predation only if the induced defense incurs costs in the absence of predators. Pettersson and Bronmark (1997) tested the hypothesis that the advantage of a deeper body comes at a cost of reduced growth in the absence of predators. They found that at high carp density shallow-bodied forms grew significantly faster than deep-bodied forms (an effect not observed at low carp densities). This suggests a density-dependent mediated tradeoff between predator-present vs. -absent environments for the induced form; therefore, plasticity of body form may be an adaptation to heterogeneity in predation among lakes. Two questions remain to be addressed. First, it is not clear why a slender body form is advantageous in the absence of predators. Does the advantage come specifically from being slender (and if so, why) or from changes in some other correlated trait? Second, why does high food abundance also induce a deep-bodied form (Holopainen et al. 1997)? Perhaps carp respond to cues that indirectly indicate predation, such as increased prey abundance owing to reduced carp abundance. An alternative hypothesis is that high food abundance may result in plastic responses in life history that are correlated with a deeper body.

Threespine sticklebacks also exhibit considerable phenotypic variation among populations (McPhail 1994), but only recently was the contribution due to morphological plasticity studied. Two morphologically and genetically divergent sister species of threespine sticklebacks (commonly referred to as benthics and limnetics) are plastic in response to rearing on benthic or pelagic prey. The two species coexist in five coastal lakes in British Columbia, Canada, and have recently diverged from a marine ancestor after colonizing young lakes created after the glacial retreat sometime in the last 11 000 years (McPhail 1994). Variation in mouth, gill raker, and body-size traits confer advantages to each species in its native habitat (Schluter 1993, 1995). Day et al. (1994) collected the progeny of both species and performed a controlled reciprocal transplant experiment by rearing half of each species on either benthic prey (live *Tubifex* worms) or pelagic prey (live *Artemia* nauplii). Both species showed plastic responses in four out of six morphological traits, with broader reaction norms found in the limnetics. Both species partially developed the other's morphology when reared on the alternate diet. In a second experiment, Day and McPhail (1996) reared the progeny of limnetics on benthic prey to explicitly test if the induced benthic-like morphology could improve foraging efficiency on benthic prey compared with control groups of limnetics reared on zooplankton. Foraging efficiency increased significantly in the induced benthic form as predicted. This experiment allowed foraging efficiency to be decomposed into a component due to morphological plasticity (primarily influencing prey handling time parameters) and a part due to behavioral plasticity (primarily influencing search time efficiency) and demonstrates an interaction between morphological and behavioral plasticity. It also shows

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Table 3. Predicted morphological responses induced by littoral vs. pelagic conditions for six common ecomorphological traits in fishes.

	Treatment conditions		
Features	Littoral	Pelagic	Expected function
Paired fins			
Length or width	Larger	Smaller	L: three-dimensional maneuverability
Location	Lower	Higher	P: reduced drag
Body form			
Shape	Robust	Slender	L: burst swimming
Head	Larger	Smaller	P: reduced drag
Caudal peduncle			
Dorsal–ventral	Deeper	Shallower	L: burst swimming
Lateral cross section	Compressed	Widened	P: cruising
Length	Shorter	Longer	
Mouth orientation			
	Subterminal	Terminal	L: substrate prey capture
		Upturned	P: water column – water surface prey capture
External–internal architecture of mouth and jaws (bones and muscles)			
	Larger	Smaller	L: processing larger harder prey
	Robust	Reduced	P: processing smaller softer prey
Gill raker architecture			
Number and length	Fewer, short	More, long	L: reduced clogging by sediment
Interraker gap	Larger	Smaller	P: planktivory

Note: The right-hand column describes the expected functional utility of the phenotypic state for the resulting littoral (L) and pelagic (P) forms. Function was inferred from either ecomorphological studies of fishes or from comparative approaches that show a convergence on a particular phenotype by taxa that inhabit similar environments (see text for references).

that only with careful experimental design can traits that confer advantages be identified. Although the reciprocal test using the benthic species has not been performed, diet-induced phenotypes have been shown to have consequences to foraging performance even in less divergent phenotypes that coexist in a single variable stickleback population (Robinson 2000). More such direct tests of whether induced morphological changes have positive influences on performance are required.

Prediction 2. Induced morphological responses conform to functional expectations

Plastic morphological responses are likely adaptive if norms of reaction are in directions that are expected to improve performance. Our understanding of the mechanics and function of body form in fishes is now making it possible to qualitatively predict what forms will confer advantages under particular conditions. These expectations come from two sources: studies on the functional and ecological morphology of fish body form (Norton et al. 1995; Walker 1997) and comparative analyses of body form among divergent species believed to be specialized for either pelagic or littoral habitats (Webb 1984*a*, 1984*b*). The convergence on a specialized body form by different taxa that inhabit similar environments is strong evidence of a role played by natural selection in the evolution of body form. This approach forms the core of the comparative method because no random evolutionary processes are expected to regularly result in such phenotypic convergence (Schluter and Nagel 1995; Robinson and Schluter 2000). By extension, the adaptive divergence of species between environments can be used to make predictions about induced responses to these same environments within a species (e.g., Travis 1994). This assumes that evolutionary constraints within taxa are similar to those among taxa and that plasticity can evolve. Insufficient additive genetic variation in reaction norms would violate this assumption. We consider evidence of genetic variation in plasticity below and only note here that it is present in all studies that have tested for it.

We make qualitative predictions about inducible variation for six general features of fish morphology in response to littoral and pelagic conditions (Table 3). These features are as follows: (1) the size and location of paired fins (pectoral and pelvic fins); (2) overall body shape, including body depth (and variation in dorsal and anal fin heights) and head size; (3) caudal peduncle size and shape; (4) the orientation of the mouth; (5) the size of external and internal mouth elements (bones and muscles); and (6) gill raker architecture (number, length, and size of the gaps among adjacent rakers).

The last column of Table 3 provides a functional interpretation for character states in each environment. For example, paired fins are predicted to be larger (in length and (or) width) and found lower on the body in littoral than pelagic forms because increased fin size and lower orientation improves hovering and maneuverability in three dimensions (Webb 1984*a*). This is thought to be useful for navigating and searching for cryptic prey in the structurally complex littoral environment compared with the open waters of the pelagic habitat. A more slender body form, on the other hand, is predicted to reduce drag during sustained cruising through the pelagic habitat in search of patchily distributed planktonic prey (Webb 1975). A deeper body form improves fast-start capacity, potentially useful in littoral habitats where prey are often larger and faster and where predators deploy ambush tactics rarely used in the pelagic habitat (Walker 1997). The caudal peduncle is the primary structure driving

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Table 4. Summary of plastic morphological responses induced by littoral and pelagic conditions from 18 cases involving 66 norms of morphological reaction (Table 2, Appendix A).

Feature	Sunfish	Whitefish	Minnows	Sticklebacks	Perch	Salmon	Total
Paired fins	2/2	4/5					2 (6/7)
Body form	2/2	6/8	3/3	3/3	1/1	4/5	6* (19/22)
Caudal peduncle	1/2	0/1					1 (1/3)
Mouth orientation	4/4	1/5		1/1		1/1	3 (7/11)
Mouth and jaws	5/5	0/4		0/1		1/1	2 (6/11)
Gill rakers	0/1	6/7		2/2		2/2	3 (10/12)

Note: Data are tallied by morphological feature (Table 3) and family. The fraction in each cell reflects the number of observed plastic responses that were in the expected direction relative to the total number of plastic responses tested, pooled among species and populations. The numbers in the right-most column are the total number of families in which the expected plastic responses were commonly observed, and the fraction (in parentheses) refers to the number of expected responses out of the total number of plastic responses observed for that trait pooled among families.

*Binomial one-sided $p < 0.015$.

the caudal fin, and its form in part dictates the energy efficiency and power of the caudal stroke. A shortened caudal peduncle that is deep (dorsal–ventral) and laterally compressed provides better burst swimming, useful in the littoral habitat. A longer caudal peduncle that is shallow and widened laterally requires less energy for sustained cruising in the pelagic habitat. Benthic foraging usually involves picking-off prey from, or biting into the substrate, an activity facilitated by a subterminal mouth, whereas pelagic foragers often consume prey from the water column with terminal or upturned mouths (Keast and Webb 1966). We also predict that larger and more robust mouths and associated skeletal and muscular features are more efficient for processing the larger, harder littoral prey compared with the smaller pelagic prey (Wainwright et al. 1991). Although the direct function of gill rakers in planktivory is unclear (e.g., Langeland and Nost 1995; Sanderson et al. 2001), comparative studies indicate that planktivory is correlated with many, longer, and closely spaced gill rakers (Kliewer 1970; Magnuson and Heitz 1971; Sanderson et al. 1991). These relationships are so common both among and within taxa that their functional interpretation is becoming less controversial, although additional direct performance tests will be useful (Norton et al. 1995).

We evaluated the morphological responses observed in the 18 cases of plasticity involving littoral and pelagic conditions (Table 4) by tallying up the number of "predicted" vs. "novel" plastic responses for each morphological feature and family (Appendix A). Data on induced morphological changes was available for 66 norms of reaction related to the six focal morphological traits (Table 3; traits: body form, mouth location, gill rakers, body or head depth, paired fins, caudal peduncle, and jaw and mouth size in Appendix A). Forty-nine of the induced morphological responses (74%) were in expected directions ($p = 0.0001$, one-sided binomial test against a proportion >0.5). Although each norm of reaction here is unlikely to be independent of others from that study, it is difficult to know a priori which reaction norms are independent because norms of reaction may or may not be integrated (correlated; Schlichting and Pigliucci 1998). However, this proportion is statistically robust even when the total number of reaction norms considered is reduced from 66 to 16 (one-sided $p = 0.04$). There is some evidence of novel induced responses in mouth orientation and size in whitefish (1/9, one-sided $p = 0.02$).

Prediction 3: Convergence on specific norms of reaction

We found a family-level convergence on the predicted norms of reaction in response to littoral and pelagic conditions for general body form (e.g., slender vs. robust; Table 4). Members from all six families exhibited the expected plastic response in body form (6/6 families, one-sided binomial p value = 0.015). Empty cells reflect only that the appropriate tests have yet to be performed (Table 4). Additional studies that explicitly describe morphological responses to littoral and pelagic conditions are required to test for convergence on reaction norms for the remaining traits.

Although these results are preliminary because of the relatively small number of studies available for analysis, they indicate that body form responds in the same predictable way to littoral and pelagic conditions among species in six families. The only explanation for replicate patterns of plastic responses is that divergent selection has favored the same pair of alternate phenotypes in these two lake habitats (Robinson and Schluter 2000). Thus, divergent selection imposed between these environments can cause genetic changes in plastic as well as in developmentally canalized traits (Schluter 2000).

Convergence on similar reaction norms need not occur for different taxa that experience similar environments. For example, a reasonable prediction would be consistent responses towards a more fusiform body form in fish reared under increased water velocities to reduce drag. Pakkasmaa and Piironen (2001) did not find consistent responses by brown trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*) reared under low vs. high water velocity (see also Imre 1999). Salmon reared in fast flow were more robust than those reared in slow water, whereas brown trout showed the opposite response, demonstrating a taxon-specific response despite their common origins in a variable stream environment. These differences may reflect adaptation to microhabitats within streams at a finer scale than we recognize or that taxon-specific constraints influence the evolution of morphological plasticity (Witte et al. 1990).

Genetic variation for plasticity

Additive genetic variation is a prerequisite for selection to have an evolutionary consequence in any trait being considered. What evidence of genetic variation exists for morphological plasticity in response to littoral and pelagic conditions? With so few studies focused on adaptive plasticity in

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northern fishes, it is not surprising that there are even fewer tests of heritable genetic variation in plasticity. We know of only five tests, and all have confirmed its existence. Four studies used fishes from lakes (e.g., threespine sticklebacks, sunfish, and perch) and the remaining study used a riverine population of chum salmon (*Oncorhynchus keta*).

The study by Day et al. (1994) of plasticity in threespine stickleback species-pairs reared on different diets demonstrated genetic variation in plasticity at two levels. First, the limnetic species showed greater morphological plasticity than the benthic species. These species have only recently diverged from a common marine ancestor (McPhail 1994), and therefore, this variation is unlikely to have arisen by mutation in such a short period. Instead, it seems more likely that variation in plastic responses existed in the ancestral marine population that has been differentially selected for in the modern species. Second, Day et al. (1994) demonstrated significant family level effects on the form of plastic responses in both species. Additive genetic variation in morphological plasticity occurs both within and among populations of threespine sticklebacks. Heritable genetic variation in morphological plasticity has also been demonstrated in chum salmon (Beacham 1990).

Robinson and Wilson (1996) found significant evidence of differences in the plasticity of littoral and pelagic forms of pumpkinseed sunfish reared in pelagic and littoral enclosures. A reanalysis of this data set has also shown substantial differences in the coordination of the plastic responses for 20 traits between the two forms (Schlichting and Pigliucci 1998). Pelagic forms show a greater coordination of plastic responses among body-form traits compared with littoral forms (measured as the number of across rearing environment correlations involving pairs of morphological features; unpublished data). Because both forms were reared between the same pair of environments, this difference in the integration of induced responses between forms represents genetic variation in the integration of plastic responses by the two types of sunfish. Hegrenes (1999) also documented variation in the plasticity of mouth traits in response to diet among populations of both pumpkinseed and bluegill sunfish.

Lastly, the analysis by Hjelm et al. (2001) of morphological plasticity in the Eurasion perch (*Perca fluviatilis*) demonstrated changes in body form in response to littoral and pelagic conditions as expected and that the form of the reaction norms varied among three local lake populations of perch. Although such results are currently limited to only a few taxa, we know of no case where genetic variation for plasticity has not been demonstrated when explicitly tested, and therefore we expect similar results in other taxa.

Evolution of adaptive plasticity

The convergence on similar norms of morphological reaction in different taxa exposed to similar lake environments is strong evidence that natural selection has molded these responses (Robinson and Schluter 2000). The following conditions favor the evolution and maintenance of adaptive plasticity in northern freshwater fishes: (1) individuals experience environmental variation; (2) phenotypes experience fitness tradeoffs across different environments; and (3) individuals have reliable cues to match an induced phenotype to the environment (Travis 1994). We cannot discuss possible constraints on the evolution of adaptive plasticity in this system because so few studies are currently available (Witte et al. 1990; DeWitt et al. 1998).

The littoral and pelagic environments reflect distinct and important environmental niches for many fishes (e.g., Smith and Todd 1984; Robinson and Wilson 1994; Schluter 1996). Single lakes can contain both niches (patches within lakes), or variation can occur among lakes that are more or less dominated by littoral or pelagic conditions (Robinson et al. 2000; Schindler and Scheuerell 2002). This complicates the analysis of the scale at which fish experience environmental variation. We return to the question of scale after we review the evidence for tradeoffs and cues.

Recent studies have demonstrated a significant interaction between phenotype and environment on fitness in a number of fishes (Schluter 2000). The superiority of a phenotype in its native environment vs. others is often used to test if divergent forms experience fitness tradeoffs between environments. Levins (1962) noted that such reciprocal transplant experiments modified to include phenotypic intermediates could indicate when divergent selection favors the evolution of specialized forms (although such tests are still rare; Schluter 2000). Tradeoffs have been demonstrated between recently diverged species (Schluter 2000) and sometimes between morphs from single populations (Robinson et al. 1996; Smith and Skulason 1996; Proulx and Magnan 2002). Parallel patterns of phenotypic divergence between a wider array of species and forms in postglacial lakes is also strong evidence that natural selection has favored the evolution of specialization in the face of environmentally mediated fitness tradeoffs (Robinson and Wilson 1994; Schluter 1996). Although it can be difficult to specifically identify the traits that influence fitness (Robinson 2000), these results indicate that specialization in either of these lake habitats can come at the expense of reduced performance in the other.

The specific cues that fish use to initiate plastic responses to environmental variation have received little attention. Laboratory studies have shown that diet can have a strong influence on fish morphology during development (Day et al. 1994; Wimberger 1994; Mittelbach et al. 1999). Possible aspects of prey that induce morphological responses are prey size and hardness, ease of capture, location, and whether prey are located on a substrate or are free-swimming. Other cues may also induce morphological responses. Hegrenes (1999) found that laboratory diets induced morphological changes only in the head of sunfishes, with little effect on other body-form traits, in contrast to a study by Robinson and Wilson (1996) that found plasticity in body morphology of juvenile sunfish reared in different pond environments. On the other hand, diet manipulations alone can induce changes in head, body, and fin traits in other fish (Meyer 1987; Wimberger 1992). This suggests that cues that induce morphological changes can be species-specific. Plasticity in sunfishes may respond not only to cues arising from handling and processing different prey types (Mittelbach et al. 1999), but also to cues that result from search behavior used in different lake environments (such as cruising vs. swimming frequently interrupted by hovers and fast starts; Ehlinger and Wilson 1988). Although we rarely know which cues induce plastic responses, we expect that prey features and the strategies

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used to find and handle prey vary consistently between littoral and pelagic habitats (see also Webb 1984*a*). This suggests that an array of possible cues is available to reliably match induced phenotypes to local environmental conditions.

Environmental variation within and among postglacial lakes

We now return to the first condition that the evolution of plasticity requires environmental variation. This condition has two components: different patches occur in time or space and genotypes unpredictably encounter these patches. Littoral and pelagic habitats occur within and among many contemporary postglacial lakes (Robinson et al. 2000; Schindler and Scheuerell 2002). Understanding the evolution of adaptive plasticity in these lakes will require an evaluation of current and possible historic conditions. We can imagine four scales at which spatial and temporal variation may have favored the evolution of morphological plasticity in northern taxa: (1) fish may currently face unpredictable environmental variation; (2) fish may have experienced variation within and among newly created lakes during the colonization of postglacial environments; (3) the environments of refuge lakes during the glacial period may have been temporally variable; and (4) northern fish experienced large-scale environmental variation repeatedly during the 20 or so glacial–interglacial periods over the last two million years (Pielou 1991; Robinson and Schluter 2000). There is little evidence available to assess the third and fourth hypotheses; therefore, we limit discussion to the first two.

Contemporary patterns of environmental variation

Our first hypothesis is that contemporary lake environments provide either spatial or temporal variation that favors functional plastic responses. Many fish taxa experience regular ontogenetic niche shifts between these habitats (e.g., Klemetsen and Dahl-Hansen 1995). Theory suggests that over ontogeny, individuals should shift habitat and prey use to optimally balance foraging returns and predation risk, both mediated by body size (e.g., Werner and Gilliam 1984; Grand and Dill 1996). Could such environmental shifts favor adaptive plasticity? Ontogenetic habitat or dietary shifts are often related to size, and shifts are expected to be relatively consistent among similar-sized individuals within a population. When prey and predator abundance are relatively constant, selection should favor optimal body forms at sizes that provide the best match with environment, and plasticity is unlikely to be advantageous. However, if foraging returns or predation risk vary unpredictably over time, then ontogenetic (and morphological) plasticity could be favored.

Fishes of postglacial lakes may also experience unpredictable environmental variation on average every few generations because of relative changes in the richness and abundance of resources in different lake environments. This could be due to environmental factors that drive relative prey abundance in different habitats, such as seasonal or longer environmental fluctuations or the arrival or local extinction of a competitor. The few examples that we know of share the property that the habitat shift was related to the invasion (or presence) or extinction of another potential competitor. For example, Lindsey (1981) used a comparative approach to detect rapid shifts in gill raker traits in whitefish that appeared to depend on the presence and habitat use of other coexisting whitefish taxa. Habitat shifts were inferred from the generally strong correlation between gill raker number and length and diet and habitat use. Nilsson (1963) studied patterns of resource use by Arctic char and brown trout isolated in lakes and found that both species preferred benthic prey. The two species show more segregated diets in lakes where they coexist, a pattern most strongly observed in hydroelectric impoundments where the abundance of benthic invertebrate fauna is already limited. The trout diet continued to be dominated by benthic prey, whereas adult char appear to switch their diet primarily to pelagic zooplankton. Tremblay and Magnan (1991) have observed similar diet shifts in brook trout in response to the presence of white sucker (*Catostomus commersoni*). Crowder (1986) found evidence that juvenile bloaters (*Coregonus hoyi*) from Lake Michigan dramatically reduced their zooplanktivorous interval over a 20-year interval following the invasion of zooplanktivorous alewife (*Alosa pseudoharengus*). In all of these cases, competition was inferred rather than directly tested.

Habitat and diet shifts have also been related to the local extinction of a competitor. Wainwright et al. (1991) suggested that the extinction of bluegill sunfish in Wintergreen Lake resulted in the competitive release of juvenile pumpkinseed sunfish. The absence of predators in the system allowed the pumpkinseed population to rapidly increase, causing the collapse of their dominant snail prey. Aquatic insect larvae subsequently dominated the diet, and the pumpkinseeds developed less robust pharyngeal jaws compared with other populations feeding on snails. The reintroduction of bluegill to the lake could reduce pumpkinseed abundance, resulting in an increase in snails and perhaps another diet switch.

Theoretically, predation can also cause populations to shift habitats because of flexible behavioral responses to predation or top-down trophic dynamics. For example, in the pumpkinseed case just described, the arrival of a predator could cause the pumpkinseeds to shift habitats or could reduce pumpkinseed density, in turn releasing the snails from sunfish predation. An increase in snail abundance could favor a shift in pumpkinseed diets back to snails. We know of no natural example of this, although significant habitat shifts have been observed in fish populations that experience intensive human harvesting (e.g., Klemetsen and Dahl-Hansen 1995). The invasion or extinction of a competitor (or possibly predator) may be unpredictable, particularly when the competitor or predator is at the edge of its natural range. Lastly, habitat coupling in lakes can cause changes in the relative resource profitability between lake habitats and potentially resource use by fishes (Schindler and Scheuerell 2002). Fish are one of the primary agents of energy and nutrient exchange between littoral and pelagic habitats and so may cause shifts in resource abundance that feed back and result in regular diet shifts that may favor the evolution of plasticity. Empirical evaluation of the role of competitors, predators, and habitat coupling in the temporal variation of resources between lake habitats requires long-term studies that are only in their infancy.

Historic patterns of environmental variation

Our second scenario proposes that postglacial fishes experienced significant spatial variation in environmental condi-

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tions among lakes during their rapid colonization after the last glacial retreat beginning 18 000 years ago in North America (Pielou 1991; Mandrak 1995). A mosaic of lakes was formed that may have varied in the relative profitability of habitats within as well as among lakes. Fish that colonized young postglacial lakes are believed to have had short and variable periods of migration through relatively limited corridors generated by changing watershed boundaries, isostatic rebound, and short but torrential flood events (Hocutt and Wiley 1986). Infrequent and short colonization opportunities could have limited the number and order of immigrants that arrived in a lake (Mandrak 1995). Differences in local fish communities would have also contributed to variation in local resource abundance among lakes. Variation in invertebrate prey fauna also occurred because of the effect of local abiotic conditions, time lags specific to individual lakes (Dodson et al. 2000), local species interactions (Langeland et al. 1991), vicariant patterns of colonization (Cox and Hebert 2001), and the proximity of source populations (Sheldon 1984). We propose that these conditions contributed to considerable variation in the resources among habitats within newly created postglacial lakes.

Fish sequentially colonizing these lakes encountered unpredictable environmental conditions that could have favored the evolution of adaptive plasticity for two reasons. Plasticity can facilitate shifts between habitats in the face of unpredictable habitat-specific resource profitability and would have been favored because it conferred a survival advantage within lakes. Second, plasticity may also have been favored because it increased dispersal among lakes. Cwynar and MacDonald (1987) have shown how colonization over 2200 km of postglacial habitat favored an evolutionary increase in the (nonplastic) dispersal traits of Lodgepole pine seeds. If phenotypic plasticity is positively related to dispersal in postglacial fish taxa and was favored by selection during the colonization of postglacial lakes, then we predict that populations at the most distant location from their glacial refuge should on average be more plastic than those near the location of their last refuge.

Plasticity and divergence in northern freshwater fishes

To what extent has phenotypic plasticity influenced the evolution of northern fish taxa? Wright (1931) suggested that plasticity would retard adaptive divergence by obscuring underlying genetic variation from selection acting on environmentally induced phenotypes. This "negative effect" hypothesis is still regularly invoked (e.g., Adkison 1995; Schlichting and Pigliucci 1998). Alternatively, plasticity may enhance opportunities for genetic divergence. First, plasticity may reduce the probability of extinction of a founding population in a novel environment, which then permits genetic variation to potentially come under divergent selection (Smith and Skulason 1996; Robinson and Dukas 1999). Second, plasticity may permit rapid divergence among populations; for example, when a plastic developmental system capable of producing alternate inducible forms becomes canalized (as a result of selection or drift) for different phenotypes among populations (West-Eberhard 1989; Schlichting and Pigliucci 1998). Third, induced phenotypic responses can increase variation in fitness-related traits of a population that permits a rapid response to direct selection among genotypes that vary in direction and magnitude of inducible responses and indirect selection on other correlated traits (e.g., Milligan 1985).

Our analysis indicates that the fishes of postglacial northern lakes exhibit considerable plasticity in a variety of morphological and, although we haven not reviewed it here, probably life history and behavioral traits (see Introduction). Schluter (1996) and Bernatchez and Wilson (1998) have shown that many of these same taxa are rapidly diverging and in some instances forming new species. These observations are inconsistent with the view that plasticity only retards evolution and, instead, are consistent with the idea that plasticity either has no effect or a positive effect on divergence in postglacial fishes.

Phenotypic plasticity may be positively related to adaptive radiation and speciation in other fish taxa. As detailed above, freshwater threespine sticklebacks exhibit considerable morphological plasticity (Day et al. 1994; Day and McPhail 1996) along the same phenotypic axes that has permitted rapid divergence in freshwater habitats (Bell and Foster 1994), raising the possibility that inducible responses have biased paths of adaptive divergence. Cichlids also provide one of the most dramatic examples of adaptive radiation known, and we have found that cichlids provide 83% (15 out of 18 studies) of all nonpostglacial examples of morphological plasticity in our survey of the literature. These 18 studies involve 14 species of freshwater fish from four families (Centrarchidae, Cichlidae, Goodeidae, and Poecilidae). Fourteen of the 15 cichlid studies involve treatments related to littoral and pelagic conditions. Most studies of old world cichlids have examined morphological plasticity in mouth or pharyngeal jaw traits in response to diet (e.g., Witte et al. 1990; Huysseune 1995), whereas studies with new world cichlids have also noted plasticity in body form (Meyer 1987; Wimberger 1994). African cichlids are believed to have colonized watersheds from west to east (Farias et al. 2000), perhaps putting them under selection during colonization that also favored morphological plasticity. These examples share the common features of rapid adaptive divergence and radiation in phenotypic directions congruent with morphological plasticity observed within species (Losos et al. 2000 provide an additional example in the *Anolis* lizard radiation). A positive evolutionary influence of plasticity on divergence is conceptually attractive because the modification of a plastic developmental system to one producing limited phenotypic outcomes provides one mechanism whereby populations can rapidly diverge (West-Eberhard 1989; Wimberger 1994; Schlichting and Pigliucci 1998). The consequences of this to the evolution of pre- and post-zygotic isolating mechanisms are of great interest to evolutionary biologists who focus on species formation during adaptive radiation (Smith and Skulason 1996).

This approach cannot distinguish between plasticity being a cause or a consequence of divergence. However, the canalization model suggests two additional predictions. The adaptive morphological divergence of closely related species that use different environments should parallel the plastic morphological responses induced by these environmental conditions within each species. This appears to be the case for both the threespine sticklebacks (Day et al. 1994) and some

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cichlids (Wimberger 1994). Second, plastic responses in extant ancestral taxa should encompass much of the morphological diversity found in descendent taxa. This assumes that divergence is sufficiently recent that mutation has not contributed significantly to either the diversity observed among descendent taxa or affected plastic responses in the ancestral taxa. Considerable morphological plasticity is found in a basal riverine member of the African cichlids, *Hemichromis guttatus* (K.J. Parsons, unpublished data), and in the presumed ancestor (*Amphilophus citrinellum*) of a species flock of cichlids in Lake Apoyo, Nicaragua (Barlow and Munsey 1976; K.J. Parsons, unpublished data). The ancestral marine threespine stickleback exhibits considerable morphological and life history plasticity when reared in fresh water, although the form of the reaction norms has not been studied in any detail. In none of these cases has the range of plastic morphological responses in the extant "ancestral" species been compared with variation among divergent descendent taxa. The conceptual literature in evolutionary biology is beginning to shift from discussions about whether plasticity can have a positive influence on adaptive divergence to discussions about the conditions that favor positive vs. negative effects of plasticity on divergence (e.g., Schlichting and Pigliucci 1998). Fishes undergoing the earliest stages of adaptive divergence may be ideal systems in which to address these questions.

The morphological plasticity exhibited by fishes from northern postglacial lakes is both ecologically and evolutionarily interesting because it can influence resource and habitat use, species interactions, and the evolution and hence identification of stocks that vary in plastic and other traits. Using a meta-analysis of the available literature, we have quantified a strong relationship between morphological plasticity and environmental conditions associated with littoral and pelagic habitats in lakes (Robinson and Wilson 1994; Smith and Skulason 1996). Convergence on similar inducible responses in body form across populations and taxa exposed to these conditions suggests that plasticity can be adaptive for differences between these two lake environments. This is one alternative to the view that morphological plasticity is a correlated response to plasticity in life history that is induced by variation in growth rate (e.g., Hindar and Jonsson 1993).

With few exceptions, there has been little direct interest in understanding the evolution, maintenance, or potential ecological and evolutionary consequences of morphological plasticity in the fishes of postglacial lakes. This is surprising given recent advances in our understanding of the mechanisms driving rapid evolution in northern fishes (Bernatchez and Wilson 1998; Schluter 2000) and the conceptual advances in the causes and consequences of adaptive phenotypic plasticity (e.g., Via et al. 1995; Schlichting and Pigliucci 1998). We hope that our analysis stimulates an interest in understanding the proximal and ultimate origins of phenotypic diversity in northern fishes to more directly examine the roles played by morphological plasticity in the ecology, conservation, and evolution of postglacial fish faunas.

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Appendix A

Table A1. Direct tests of morphological plasticity in northern freshwater fishes.

Taxa		Source[a]	No. of populations tested	Environmental conditions or treatments applied
Centrarchidae (sunfishes)				
Lepomis	*gibbosus*	L	2	Littoral vs. pelagic pond enclosures
		L	1	Hard vs. soft prey
		L	1	Experimental ponds
		L	2	Plankton vs. hard benthic
	macrochirus	L	2	Plankton vs. hard benthic
	cyanellus	L	1	Plankton vs. hard benthic
	humilis	R	1	Plankton vs. hard benthic
Coregonines (whitefishes)				
Coregonus	*clupeaformis*	L	1	Benthic lake to pelagic lake
	alvsik	R	1	Anadromous river to small lake
	artedii	L	1	Pelagic lake diet to pelagic diet
	hoyi	L	1	Wild vs. hatchery
	kiyi	L	1	Wild vs. hatchery
	alpenae	L	1	Wild vs. hatchery
	zenithicus	L	1	Wild vs. hatchery
	various sp.	L	1	Large lake to small lake
Cyprinidae (minnows)				
Carassius	*carassius*	P	1	Predation present vs. absent[d]
		P	1	Chemical cues
		L	1	Chemical cues, food abundance
Gasterostidae (sticklebacks)				
Gasterosteus	*aculeatus*	L	2	Benthic vs. pelagic prey
		L	1	Benthic vs. pelagic prey[e]
		L	1	Benthic vs. pelagic prey[e]
Percidae (perches)				
Perca	*fluviatilis*	L	3	Littoral vs. pelagic habitats
Salmonidae (salmon–trout)				
Oncorhynchus	*nerka*	L	1	Wild vs. hatchery
	kisutch	R	1	Wild vs. hatchery
		L	1	Benthic vs. pelagic prey
	fontinalis	L	1	Water velocity
Salmo	*salar*	R	1	Water velocity
	trutta	R	1	Water velocity
Salvelinus	*alpinus*	L	1	Wild vs. hatchery
	willughbii	L	1	Wild vs. hatchery

[a]Refers to the origins of the population used in the study as lakes (L), ponds (P), or rivers (R).
[b]Refers to the method used to test for morphological plasticity: reciprocal transplants (lab or field: CRT), uncontrolled transplants among lakes (UTL),
[c]The plastic morphological responses observed are grouped into those that were predicted vs. those that were novel. Note that separate reaction norms traits: body form (BF), pharyngeal jaws (PJ), mouth orientation (M), gill rakers (GR), fins (F), body depth (BD), paired fins (PF), caudal fin (CF), caudal
[d]Survival or growth performance of induced forms assessed under predation.
[e]Foraging performance of induced forms assessed on different prey.

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Test method[b]	Plastic response[c] Predicted	Novel	Reference
Field CRT/CG	BF, PF, CP		Robinson and Wilson (1996)
Lab CRT/CG	PJ		Mittelbach et al. (1999)
Field CG	PJ		Mittelbach et al. (1999)
Lab CRT	M, PJ, J		Hegrenes (1999)
Lab CRT	M, PJ, J	CP	Hegrenes (1999)
Lab CRT	M, PJ, J, PF	GR	Hegrenes (1999)
Lab CRT	BF, M		Hegrenes (1999)
UTL	BF	BF	Loch (1974)
UTL	GR	GR	Svardson (1957)
UTL	BF, M, F	BF, PF, CP	Shields and Underhill (1993)
CG/UTA	BD, PF, GR	M, J	Todd et al. (1981)
CG/UTA	BD, PF, GR	M, J	Todd et al. (1981)
CG/UTA	BD, PF, GR	M, J	Todd et al. (1981)
CG/UTA	BD, PF, GR	M, J	Todd et al. (1981)
UTL	GR		Svardson (1957)
Lab CRT	BD		Bronmark and Miner (1992)
Lab CRT	BD		Bronmark and Pettersson (1994)
Lab CRT	BD		Holopainen et al. (1997)
Lab CRT/CG	BF, GR		Day et al. (1994)
Lab CRT/CG	HD, M		Day and McPhail (1996)
Lab CRT/CG	BF, GR	J	Robinson (2000)
Field CRT/UTL	BD		Hjelm et al. (2001)
UTA	GR		McCart and Andersen (1967)
UTA/CG	BF, M, F		Swain et al. (1991)
Lab CRT	J, HL, E		Adams et al. (2003)
Lab CRT	F		Imre (1999)
Lab CRT	CF, F	BF, BD	Pakkasmaa and Piironen (2001)
Lab CRT	BF, CF, HD, BD		Pakkasmaa and Piironen (2001)
UTA/CG	BF, J		Nordeng (1983)
UTA	GR		Frost (1965)

common garden methods (lab or field: CG), or uncontrolled transplants (lab vs. field: UTA).
from multiple forms or species are not individually identified. Abbreviations refer to the following general peduncle (CP), jaws (J), head depth or length (HD or HL), and eye diameter (E).

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PERSPECTIVE

Key principles for understanding fish bycatch discard mortality

Michael W. Davis

Abstract: The mortality of discarded fish bycatch is an important issue in fisheries management and, because it is generally unmeasured, represents a large source of uncertainty in estimates of fishing mortality worldwide. Development of accurate measures of discard mortality requires fundamental knowledge, based on principles of bycatch stressor action, of why discarded fish die. To date, discard mortality studies in the field have focused on capture stressors. Recent laboratory discard experiments have demonstrated the significant role of environmental factors, size- and species-related sensitivity to stressors, and interactions of stressors, which increase mortality. In addition, delayed mortality was an important consideration in experimental design. The discard mortality problem is best addressed through a combination of laboratory investigation of classes of bycatch stressors to develop knowledge of key principles of bycatch stressor action and field experiments under realistic fishing conditions to verify our understanding and make predictions of discard mortality. This article makes the case for a broader ecological perspective on discard mortality that includes a suite of environmental and biological factors that may interact with capture stressors to increase stress and mortality.

Résumé : La mortalité des prises accessoires rejetées à l'eau est une question d'importance dans la gestion des pêches; parce qu'elle est rarement mesurée, elle représente une source considérable d'incertitude dans les estimations de la mortalité due à la pêche à l'échelle mondiale. L'élaboration de mesures précises de la mortalité des prises accessoires nécessite des connaissances fondamentales sur les causes de cette mortalité basées sur les modes d'action des facteurs de stress. À ce jour, les études se sont concentrées sur les stress reliés à la capture. Des études récentes en laboratoire ont souligné le rôle significatif des facteurs de l'environnement, de la sensibilité au stress spécifique à la taille et à l'espèce et des interactions entre les facteurs de stress, qui accroissent tous la mortalité. De plus, la mortalité retardée est un élément important du plan d'expériences. La meilleure façon d'aborder le problème de la mortalité des prises accessoires est par une combinaison d'études de laboratoire des différentes classes de facteurs de stress pour obtenir des connaissances sur les principes fondamentaux de leur mode d'action et par des expériences sur le terrain dans des conditions de pêche réalistes pour vérifier ces connaissances et faire des prédictions sur la moralité. Il faut donc utiliser dans l'étude de la mortalité des prises accessoires une perspective écologique élargie qui considère une série de facteurs environnementaux et biologiques qui peuvent interagir avec les facteurs de stress lors de la capture pour accroître le stress et la mortalité.

[Traduit par la Rédaction]

Introduction

Mortality of fish released after capture (discarded bycatch) because of harvest restrictions (i.e., number, size or sex limits, or incidental catch as nontarget species) is one of the most significant issues affecting marine fisheries management today. Total discarded bycatch has been estimated to be approximately one-quarter of the worldwide fisheries catch, with discard mortality representing a large source of uncertainty in estimates of fishing mortality (Alverson et al. 1994; Pascoe 1997). Discard mortality rates in specific fisheries are rarely known, and general methods for estimating discard mortality rates in a wide range of threatened fisheries are not yet available. Although a few field studies have measured discard mortality by holding fish for short time periods after capture or by using tag and recapture methods, they resulted in qualitative mortality estimates with limited accuracy. Development of accurate quantitative methods to measure discard mortality in the field requires fundamental knowledge of why fish die after being discarded and how to measure this endpoint under a wide range of realistic fishing conditions.

In recent years there have been several workshops and review papers defining the discard problem, outlining specific actions that have been taken, and suggesting possible solutions for the future (Alverson et al. 1994; Pascoe 1997; Hall et al. 2000). Solutions to the discard problem have focused on preventing bycatch from landing on deck by avoiding ar-

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eas containing potential bycatch, modifying fishing gears in ways that reduce bycatch capture, and allowing for bycatch to escape through grids, panels, or increased mesh sizes (e.g., Kennelly and Broadhurst 1995; Broadhurst 2000). Although a great deal of progress has been made in reducing discards through improvements in fishing gear selectivity, there remains the problem of undetected bycatch mortality for fish that escape gear or are discarded after landing on deck. In this paper, we address the question of discard mortality and leave the problem of mortality in fish escaping fishing gear for a future discussion.

Because discard mortality results from the interactions of animals and fishing gear, efforts at resolution of the discard problem should rely on a combination of social, economic, engineering, and biological solutions. Fishing is conducted under social and economic constraints with gear that has traditionally been designed to modify fish behaviour in ways that facilitate capture. For fixed gear (hook and line, pots and traps), fish are attracted to gear by baits, which elicit chemosensory and gustatory responses resulting in capture. For towed gear, the avoidance response of fish is used to herd fish into the cod-ends of nets. Although seines are not towed, they also use avoidance behaviour to herd fish for capture. Gill nets act as passive capture devices, which are generally not detected by fish before capture. Fishing gear has been modified to use fish behaviour for decreasing capture of bycatch species. Relatively little attention has been paid to the role that biology and ecology of fishery resources might play in reduction of mortality in fish that are captured and discarded, especially the interaction of fishing practices with environmental factors (light conditions, temperature, air exposure, anoxia, sea conditions, and pressure changes) and biological factors (fish size and species, behaviour, physiology, and potential mortality).

This perspective is not meant to be an exhaustive discussion of the general fish discard problem, but rather to highlight key principles that underlie stress and mortality in discarded fish bycatch. These principles are also of general ecological interest and include the following: (*i*) increased mortality caused by interactions of stressors; (*ii*) the importance of environmental factors; (*iii*) species- and size-specific differences in sensitivity to stress; and (*iv*) delayed mortality after discarding. Although field studies could be made of the seemingly unlimited interactions among specific fishing gear types, environmental conditions, and fish species, we are more likely to uncover patterns and generalities for discard mortality with systematic laboratory experiments than by making random combinations of conditions in field experiments. It would be prudent and more efficient to understand principles controlling discard mortality and then to correlate innovative behavioural and physiological measures of stress and mortality with potential discard mortality in the laboratory. These assays of mortality could then be used in situ under all types of fishing conditions to predict discard mortality and evaluate new fishing methods designed to reduce or eliminate discards (Schreck 1990; Davis et al. 2001).

Capture and gear effects

All major fishing gear types involve some degree of injury to fish by internal and external wounding, crushing, scale loss, and hydrostatic effects, with the severity of injury dependant on gear type. Contact among fish in gear ranges from little in hook and line and gill-netting to moderate in traps and abundant in trawling and purse-seining with brailing. Fish interactions with gear vary widely, e.g., wounding from hooking, scraping in trawls, seines, brailing nets, and traps, and gilling in gill nets. Gear deployed in surface waters does not include effects associated with depth, including differences in pressure, temperature, and light conditions. Susceptibility to injury varies with species and stressor type, although comparisons are difficult because experiments with controlled, comparable stressor conditions are rare (Olla et al. 1997). Differences in injury type among gear types is an important consideration in discard mortality, but beyond the scope of this paper.

Characteristics of fish may control discard mortality. Fish with organs (gas bladders, eyes) that inflate after capture because of pressure changes become trapped near the surface after discarding and generally experience complete mortality. They would not be considered candidates for reduction of discard mortality rates except through the use of gear avoidance and escape measures before landing on deck or when captured in shallow depths. For fish that do not have a gas bladder, or have a gas bladder or other organs that do not inflate after capture, mortality after release may be variable and sometimes quite low (Alverson et al. 1994). These fish are excellent candidates for a variety of measures that could reduce discard mortality. Mortality associated with scale loss may be greater in clupeids than in gadids (Suuronen et al. 1996*a*, 1996*b*). In round fish, mortality caused by increased temperature was greater in sablefish (*Anoplopoma fimbria*) than in lingcod (*Ophodion elongatus*) (Davis et al. 2001; Davis and Olla 2002). Flatfish (e.g., Pacific halibut (*Hippoglossus stenolepis*)) may be more sensitive than round fish (walleye pollock (*Theragra chalcogramma*), sablefish, and lingcod) to suffocation in nets by pressure on the operculum (M.W. Davis, unpublished data).

Interacting factors

The increase of stress in fish caused by interactions of stressors is probably a common occurrence (Wedemeyer et al. 1990; Barton and Iwama 1991). Stress and mortality in discarded fish from towed- or fixed-gear fisheries often results from several classes of interacting stressors (Fig. 1). These classes include capture stressors (net entrainment, mesh passage, crushing and wounding, sustained swimming until exhaustion, changes in pressure), fishing conditions (towing time, light conditions, water and air temperatures, anoxia, sea conditions, time on deck, handling procedures), and biological attributes (behaviour, size, and species) (Chopin and Arimoto 1995; Murphy et al. 1995; Richards et al. 1995).

The variety of potential stressors in fishing and the lack of controlled experimental conditions in situ makes it difficult to conduct studies that systematically examine the strength of interactions among stressors. In the field studies cited above, delayed mortality was estimated in captured fish that either were held in net pens, cages, or tanks or were tagged and recaptured to estimate survival. These methods have only been applied in a limited number of fisheries because of the inherent logistical difficulties in holding fish in the

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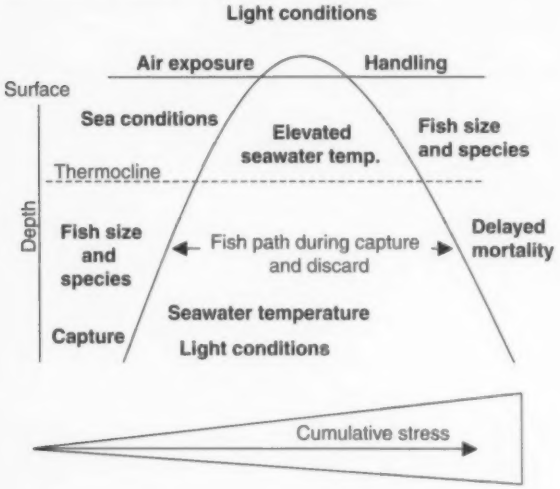

Fig. 1. Conceptual diagram of interacting factors in discard mortality for fish caught with deepwater gear (trawl, trap, hook and line). Fish caught with surface fishing gear (seine, hook and line, gill net) would not be subjected to the temperature and pressure changes associated with depth. The curved line indicates fish path at depth and the surface during capture and discard. Selected key factors are indicated in bold letters. Increasing stress level is indicated at the bottom of the diagram as interaction of factors increases initial capture stress.

field and using tagging studies to estimate bycatch mortality. The most extensive tag and recapture studies of discard mortality have been made on Pacific halibut, with the results being used in management to predict discard mortality rates based on halibut wounding observed in various fisheries (Kaimmer and Trumble 1998; Trumble et al. 2000). Although tag and recapture studies may be an accurate way to assess discard mortality, the results from these studies suffer from being obtained under a limited range of fishing, environmental, and biological (e.g., mixtures of sizes and species of animals) conditions and their interactions. Confidence in generalizing a discard mortality index to a wide range of fishing conditions is lacking until the effects of factor variation and interaction on mortality are understood. Holding fish in cages after capture to assess discard mortality also suffers from lack of generality in a range of fishing, environmental, and biological conditions.

In contrast, the role of a wide range of stressors and their interactions, which can increase stress, may be studied in the laboratory. However, it is difficult to simulate all bycatch stressors in the laboratory (e.g., catch size and composition, crushing and wounding, large changes in pressure). Although laboratory studies of discarding can be criticized for lack of realism, they allow for a systematic determination of general behavioural, biological, and physiological principles of stress response up to mortality in different species that is not possible in the field. Interactions of capture stressors (towing in a net and hooking), temperature, and air in the laboratory have been examined in walleye pollock, sablefish, Pacific halibut, and lingcod using changes in behaviour, blood physiology, and mortality as measures of stress (Davis et al. 2001; Davis and Olla 2001, 2002). In these studies, stress measured as deficits in feeding, orientation, and predator evasion and mortality increased with increased stressor intensity. Initially, capture caused stress, which was greater after towing in a net than after hooking, and then additional environmental stressors (temperature and air) increased stress reactions.

Physiological measures of stress in sablefish (plasma cortisol, lactate, glucose, potassium, sodium) increased in response to interactions of laboratory bycatch stressors (Spencer 2000; Davis et al. 2001). For example, exposure of sablefish to a gradient of bycatch stressors (increased temperature, hooking and increased temperature, and towing and increased temperature) resulted in increased plasma cortisol and lactate corresponding to the intensity of stressors. However, these plasma variables did not predict mortality, with no difference in maximum concentrations between fish that died and fish that were less stressed and survived (Fig. 2; all regression slopes not different from zero). An earlier study on the cause of death in stressed fish reached similar conclusions about predicting mortality with plasma stress variables and suggested that other physiological variables should be investigated (Wood et al. 1983). This key problem remains unsolved and physiological methods for predicting mortality are lacking.

Light conditions

Efforts to lessen or eliminate discards in trawl fisheries have centered on gear modifications that cause undersized fish or unwanted species to pass through net mesh or escape panels and not be retained in the cod-end. The success of these modifications in reducing discards often requires that fish be able to detect the gear and be volitionally guided out of the net while the targeted fish are retained (Kim and Wardle 1998). Because vision plays a dominant role in the response of at least some species to trawls, light quantity would be a limiting factor for net mesh detection (Blaxter and Parrish 1965; Glass and Wardle 1989; Walsh and Hickey 1993). Light quantity adequate for visual mesh detection is often not present, as fishing operations are commonly conducted at depths or at night. Therefore, developing effective gear modifications to reduce discards requires a clear understanding of how fish react to gear under conditions when vision is limited or not operative. Observations and measurement of fish behaviour under conditions of low light and darkness have been carried out in the laboratory with infrared illumination and video cameras sensitive to infrared light (Batty 1983; Olla and Davis 1990; Ryer and Olla 1998). Infrared technology has rarely been applied in field situations, but it has been shown to be a useful tool for measurement of animal behaviour in trawls (Matsuoka et al. 1997; Olla et al. 2000). Other possible methods currently under development for visualizing fish in trawls and traps include acoustic and laser technologies.

Observations of walleye pollock towed in a net under light and dark conditions demonstrated the value of laboratory studies for discovering key biological principles that apply to the discard problem (Olla et al. 1997). Fish in light conditions could see the net and were able to swim for up to 3 h with no resulting mortality, whereas fish in dark conditions were not able to see and respond to the net and became pinned against net meshes, ultimately resulting in mortality

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Fig. 2. Plasma physiology remains constant as mortality increases in sablefish, *Anoplopoma fimbria*. Plasma physiology (cortisol (ng·mL^{-1}) and lactate (mg·dL^{-1})) and mortality (%) for fish that were exposed to 4, 12, 14, or 16°C seawater for 30 min and air for 15 min (temperature, ●); hooking for 24 h followed by 4, 12, 14, or 16°C seawater for 30 min and air for 15 min (hooking, ■); and towing in a net for 4 h followed by 4, 12, 14, or 16°C seawater for 30 min and air for 15 min (towing, ▲). Data points are means for results at each experimental temperature treatment. Slopes of all regression lines are not different from zero. Experiments and data were described by Davis et al. (2001).

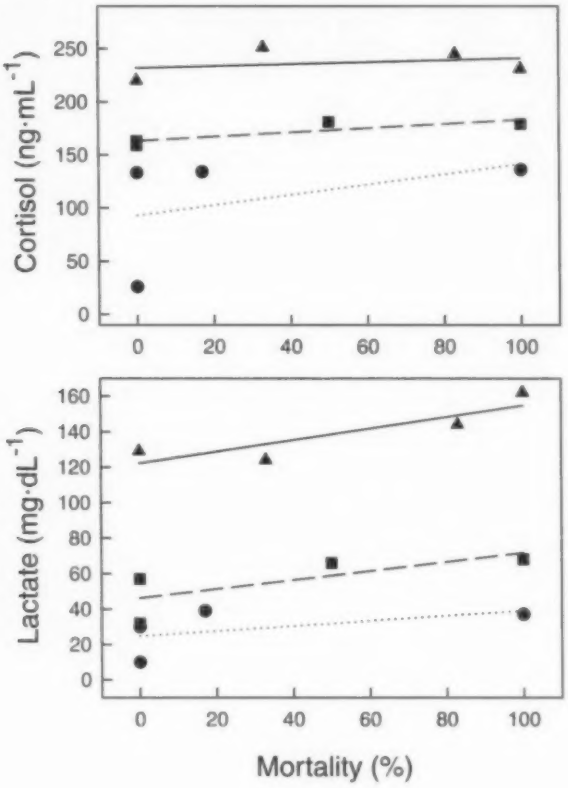
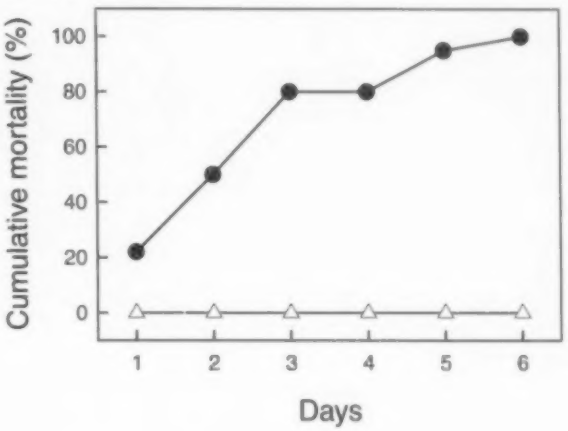


Fig. 3. Walleye pollock, *Theragra chalcogramma*, had higher cumulative mortality (%) after towing 3 h in a net in darkness (●) than in light (△). Experiments and data were described by Olla et al. (1997).



(Fig. 3). This study led to the prediction that walleye pollock captured in the field under dark conditions would not be able to orient within a trawl. Results of a field study with walleye pollock confirmed that vision played a major role in fish interactions with trawls (Olla et al. 2000). There were clear differences in fish orientation and swimming behaviour when light quantity fell below that necessary for vision-mediated swimming in a trawl. In darkness, captured fish swam less, passed along the trawl faster, and did not orient to the long axis of the trawl. This loss of orientation and swimming ability may result in less ability to escape through trawl mesh and more injury and mortality. The concordance of results between laboratory and field studies demonstrated the compatibility of these two approaches in bycatch studies.

Clearly, when escape relies on vision with active movement through openings or mesh, design of trawls to enhance bycatch escape must consider reactions under dark conditions in the field. The visual stimulus of towed fishing gear has been modeled using data from laboratory and field measurements, with predictions made on the strength of visual stimuli in trawls under various light conditions (Kim and Wardle 1998). Assessing the efficacy of trawl modifications designed to reduce discards would in part be dependant on light quantity measurements made in the gear during field trials. Differences in trawl catching efficiency between day and night have been attributed to visibility of the trawl (Casey and Meyers 1998). Differences in contrast in nets may also be important for herding fish in a trawl and increasing escape through net mesh (Glass et al. 1993). Few studies provide information about light quantity in fishing gears, making it difficult to compare results or to assign causes to observed variations in catching efficiency and reduction in bycatch.

Temperature

The additional stress and mortality resulting from the interaction of capture and exposure to increased temperature may be a widespread condition in fisheries conducted during warmer seasons of the year or in tropical areas where fish are caught in cooler deep water. Under these conditions, when fish are captured at depth by towed or fixed gear, they may be exposed to warmer water temperatures during retrieval (Olla et al. 1998). Fish may also be exposed to warmer air temperatures, regardless of capture depth. Exposure to warmer temperature results in increased body core temperature, with smaller fish warming at a more rapid rate (Spigarelli et al. 1977; Davis et al. 2001). The effects of exposure to increased temperature are well known for freshwater and marine fishes, where physiological stress and deficits in behaviour have been commonly observed (Brett 1970; Fry 1971; Schreck et al. 1997). Capture in the field under conditions of increased temperature has been observed to increase physiological stress and mortality in freshwater (e.g., Plumb et al. 1988; Schisler and Bergersen 1996) and marine fish (Barton and Iwama 1991; Muoneke and Childress 1994; Ross and Hokenson 1997).

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Exposure of sablefish held at 5°C to a range of seawater temperatures between 12 and 16°C in the laboratory resulted in loss of feeding and increased physiological stress and mortality (Davis et al. 2001). Mortality occurred after towing in a net at 5°C and exposure to 12°C or hooking at 5°C and exposure to 14°C. Exposure to 16°C resulted in complete mortality for fish that had no capture stress or had been hooked or towed (Davis et al. 2001). Similarly, towing in a net at 5°C for Pacific halibut and 8°C for lingcod caused stress, which was increased by subsequent exposure to 16°C (Davis and Olla 2001, 2002). In these three marine species, mortality rates increased with increasing seawater temperature for fish that were towed and then exposed to increased temperature, with 100% mortality reached at 16°C in sablefish, 18°C in Pacific halibut, and 20°C in lingcod (Fig. 4). These results demonstrate species-specific differences in mortality, with sablefish being most sensitive to increased temperature, followed by Pacific halibut and lingcod.

Low water temperature may alter fishing processes. Swimming speed and endurance in saithe (*Pollachius virens*), cod (*Gadus morhua*), and American plaice (*Hippoglossoides platessoides*) were reduced by low temperature (Beamish 1966; He and Wardle 1988; Winger et al. 1999). Reduced swimming speed and endurance would influence the herding of fish by sweeps, the ability of fish to maintain position in the trawl mouth, and the active escape of fish from trawls, which requires swimming through mesh or bycatch reduction devices (He 1993). Deficits in swimming performance and orientation in a trawl associated with low temperature could cause fish to be injured more frequently and may result in increased mortality. Freezing temperature on deck may also contribute to discard mortality but has not been investigated.

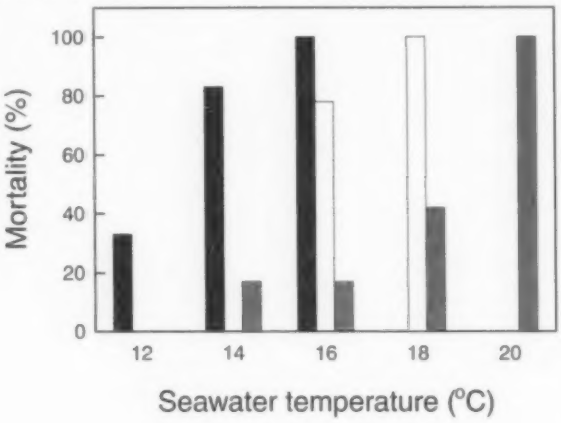
Anoxia

Lack of oxygen in towed fishing gear packed with fish, in purse seine sets, or in piles of fish and slime or mucus on deck could lead to conditions of anoxia and fish death. This subject has not been researched and deserves attention in fisheries where close packing of fish exists. The interactions of anoxia with other stressors would probably be significant also. Experiments with anoxia and discard mortality are probably best done in the field, as simulation of realistic conditions of fish packing and slime in the laboratory would be difficult.

Sea conditions

Few studies of discards have accounted for possible effects of sea state and current regimens in discard mortality. In the presence of strong currents or as sea conditions become rougher during the passage of storms, several changes leading to increased fish injury and mortality would be expected for both towed- and fixed-gear fishing. Direct interaction with trawl and longline gear resulted in scale loss, crushing, and hook damage for Atlantic halibut (*Hippoglossus hippoglossus*; Neilson et al. 1989). Similar wounding was observed in Atlantic cod caught by trawl (Suuronen et al. 1996*b*). Trawl selectivity increased and then decreased as sea state increased, with fewer haddock (*Melanogrammus aeglefinus*) retained as selectivity increased (Kynoch et al. 1999). Trawl surging associated with increased sea state altered current speeds in a shrimp trawl and led to increased trawl interaction and escapement in red snapper (*Lutjanus campechanus*) during haul-back, as changes in trawl orientation and surging caused red snapper to nose into the trawl while maintaining horizontal orientation (Engaas et al. 1999). Hauling and landing of trawls and handling time on deck would be expected to take longer in rougher seas (Maeda and Minami 1976). Increased sea motion and surging during drying and landing of trawl or pot gear would probably increase pressure on fish, although this has not been measured. Increased strain and resulting injury in hooked fish would probably occur with increased sea motion and bottom currents as gear is soaked and retrieved.

Fig. 4. Mortality (%) in sablefish (*Anoplopoma fimbria*; solid bar), Pacific halibut (*Hippoglossus stenolepis*; open bar), and lingcod (*Ophodion elongatus*; shaded bar) after exposure to 4 h towing in a net followed by increased seawater temperature (°C) for 30 min and air for 15 min. Experiments and data were described by Davis et al. (2001) and Davis and Olla (2001, 2002).



Air exposure

Exposure to air is an integral part of fish capture and increases any stress and mortality that may result from capture. Exposure times are a function of handling times on deck and can range from a few minutes when catches are small to greater than 60 min when catches are large. At least for species without gas bladder or other organ inflation, any changes in fishing practices that reduce handling time and exposure to air (e.g., reduced towing times, catch sorting times, and times to release from hooks, traps, or gill nets) would reduce discard stress and mortality, assuming that lethal stressors had not already been encountered. Exposure to air during fishing occurs over a wide range of temperatures. The differential effects of air exposure and increased temperature have generally not been separated and should be investigated in the laboratory by performing air exposures over a range of temperatures.

Relative resistance to air exposure after trawl capture was noted in winter flounder (*Pleuronectes americanus*), which did not show measurable mortality until after 45 min on

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deck (Ross and Hokenson 1997). In contrast, other discard species were more sensitive to air, with mortality occurring after 15 min in air for Pacific halibut, witch flounder (*Glyptocephalus cynoglossus*), American plaice, and saithe (Fig. 5; Hoag 1975; Richards et al. 1995; Ross and Hokenson 1997).

Lingcod were relatively resistant to air exposure at 20°C in the laboratory but had an abrupt threshold of response. No mortality was observed after 45 min of air exposure and 100% mortality occurred after 60 min in air (Davis and Olla 2002). When fish were towed in a net for 4 h and then exposed to air at 20°C, there was no mortality after 30 min of exposure and 100% mortality after 45 min (Fig. 5). In a related field study, when lingcod were captured by trawl with towing times ranging from 1 to 4 h (at 8°C) and held on deck in the air (at 13°C) for up to 60 min, mortality was not related to towing time but increased to 100% between 45 and 60 min in air, depending on total amount of catch (Steve Parker, Oregon Department of Fish and Wildlife, Newport, Oreg., personal communication).

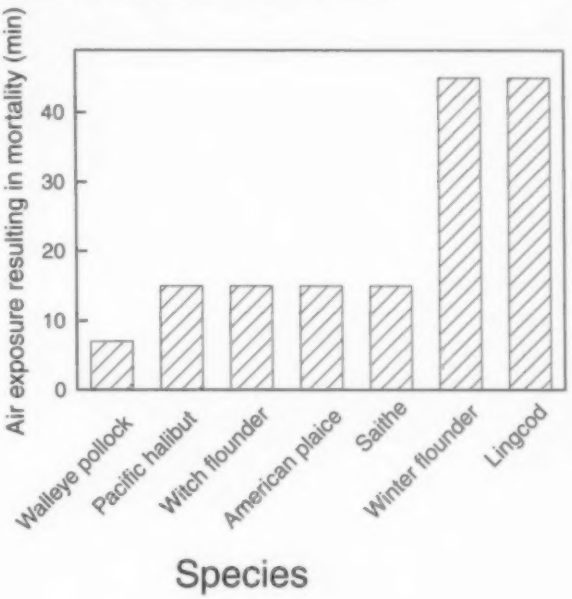
Fish size

Size-specific mortality of discards, with smaller fish showing greater mortality, is an important principle to consider in models of recruitment and yield (Neilson et al. 1989; Sangster et al. 1996; Milliken et al. 1999). Fisheries management strategies often rely on minimum-size rules for harvest, with the assumption that release of undersized fish may contribute to future recruitment and yield (Halliday and Pinhorn 2002). Target species may also be subjected to the process of "highgrading" in which smaller fish are discarded for economic reasons and larger fish are landed. Highgrading would not be recommended when smaller fish have higher mortality rates, as this would disproportionally increase discard mortality. Mortality rates of relevant size classes of fish are needed to validate the assumptions of management rules for undersized discards (Wilson and Burns 1996; Bettoli and Osborne 1998).

Smaller fish can be more sensitive to bycatch stressors and show greater discard mortality. This size effect has been observed in several species that were captured and passed through trawl gear into a net pen for observation of delayed mortality, including haddock, whiting (*Merlangius merlangus*), vendace (*Coregonus albula*), and Atlantic herring (*Clupea harengus*) (Suuronen et al. 1995, 1996*c*; Sangster et al. 1996). Increased sensitivity in smaller fish was generally attributed to fatigue from swimming as they passed down the net and greater injury from abrasion as they passed along and through the net mesh. Other studies with trawl-caught Atlantic halibut and Pacific halibut that were held in tanks after capture also found that injury and mortality was greater in smaller fish (Neilson et al. 1989; Richards et al. 1995). Size effects were also evident in longline discards, with mortality in Atlantic halibut and Atlantic cod being greater for smaller fish that were held in sea cages after capture (Neilson et al. 1989; Milliken et al. 1999).

In laboratory studies with lingcod, smaller fish reached 100% mortality after shorter exposures to air and towing and air exposure (Fig. 6; Davis and Olla 2002). Smaller lingcod reached 100% mortality also at lower temperatures when exposed to increased temperature after towing in a net, and

Fig. 5. Time of exposure to air (min) resulting in observed mortality in walleye pollock (*Theragra chalcogramma*; 14–21 cm length), Pacific halibut (*Hippoglossus stenolepis*; 60–100 cm), witch flounder (*Glyptocephalus cynoglossus*; 13–22 cm), American plaice (*Hippoglossoides platessoides*; 11–29 cm), saithe (*Pollachius virens*; 14–16 cm), winter flounder (*Pleuronectes americanus*; 9–28 cm), and lingcod (*Ophodion elongatus*; 41–67 cm). Data taken from Olla et al. (1997), Hoag (1975), Richards et al. (1995), Trumble et al. (1995), Ross and Hokenson (1997), and Davis and Olla (2002).



similar size effects were suggested in sablefish and Pacific halibut as body core temperature warmed faster in smaller fish (Davis et al. 2001; Davis and Olla 2001, 2002). Size differences in fish sensitivity to increased temperature should be widespread, based on the observed inverse relationship between the rate of body core temperature increase and fish size (Spigarelli et al. 1977).

Discard mortality of fish packed in nets may be a function of size. If catch includes a wide range of fish sizes, injury and crushing in the net, brailer, trap, or other equipment may be different than if similar-sized fish are caught together. Also the characteristics of the other species in the net may have an effect. If mixtures of individuals with hard parts (e.g., spines, shells, carapaces) and more fragile species are caught, the level of injury and mortality may be greater than when only soft-bodied individuals are present. These effects have not been investigated systematically in the field and would be difficult to study in the laboratory.

Delayed mortality

Delayed discard mortality may be common and can occur over an extended period of time after capture and release. Design of discard studies in the field or laboratory should consider delayed mortality, which may be underestimated if holding periods are not long enough. Long holding periods

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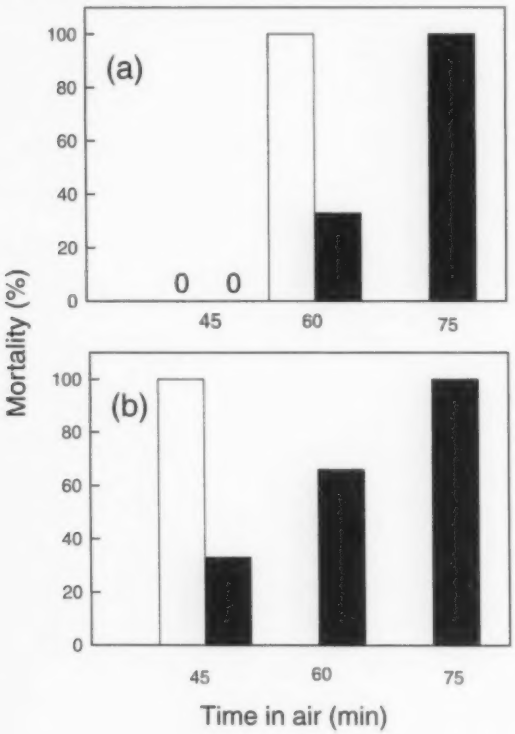
Fig. 6. Small lingcod (*Ophodion elongatus*) reached 100% mortality at lower levels of stressor intensity. Fish (open bar, small, 41–51 cm total length; solid bar, large, 52–67 cm total length) were exposed to (*a*) air for 45, 60, and 75 min and (*b*) 4 h towing in a net followed by air for 45, 60, and 75 min. Zero mortality was noted after 45 min in air for both sizes. Experiments were not performed for small fish after they had reached 100% mortality (75 min in air; 60 and 75 min tow and air). Experiments and data were described by Davis and Olla (2002).



require excellent environmental conditions, use of valid controls, and careful monitoring of fish health as overestimation of delayed discard mortality can occur when there are outbreaks of disease or parasites associated with crowding of injured fish (Neilson et al. 1989; Broadhurst et al. 1999). Although time of holding fish in the field in cages or tanks was generally limited, delayed discard mortality has been observed to vary among species. Mortality was observed up to 6 days after capture in mackerel (*Scomber scombrus*; Lockwood et al. 1983), 2 days in Atlantic halibut (Neilson et al. 1989), 4 days in plaice (*Pleuronectes platessa*), 3.5 days in sole (*Solea solea*; Van Beek et al. 1990), 14 days in Atlantic herring (Suuronen et al. 1996*a*, 1996*c*), and 10 days in Pacific halibut (Kaimmer and Trumble 1998). In laboratory studies with fish held for 60 days after stress induction, delayed mortality was observed up to 30 days in Pacific halibut, 14 days in walleye pollock, 3 days in sablefish, and 1 day in lingcod (Fig. 7; Olla et al. 1997; Davis and Olla 2001, 2002). Differences in time of delayed mortality in Pacific halibut between field and laboratory were probably caused by limited holding time in the field studies.

Delayed mortality resulting from capture has been measured in situ with tag and recapture studies in which all resulting mortality was assumed to result from capture stress. The most extensive studies developed a condition index for delayed mortality in Pacific halibut caught by trawl and hook and line, with fish being recaptured up to several years after tagging (Richards et al. 1995; Kaimmer and Trumble 1998; Trumble et al. 2000). The fish condition index, based on shipboard visual observations of wounding, has been widely used to estimate Pacific halibut discard mortality rates for management. Individual scores for Pacific halibut mortality using the condition index were limited to four quantitative levels of injury and percent mortality, including minor (3.5%), moderate (36.3%), severe (66.2%), and fleas and (or) bleeding (100%). Because this mortality index is based on visible injury, it may not be accurate under all fishing conditions. For example, when fish are exposed to increased temperature, light, air, or interactions of these factors with other capture stressors, visible injury may not accompany mortality. Behaviour may be a more sensitive measure of fish condition and potential mortality, and a behavioural index of discard mortality may be more accurate under a wide range of fishing conditions. Measurements of delayed mortality in sharks caught in gill nets have been made using a system of five levels of condition scoring based on behavioural observations of orientation and swimming ability (Manire et al. 2001). Behavioural assays of discard mortality should be studied in greater detail.

Delayed mortality of discards and fish that escape fishing gear may represent a significant source of unobserved mortality. The prevalence of delayed discard mortality indicates the presence of sublethal effects of bycatch stressors that may eventually result in indirect mortality from predation, physiological stress, or disease. Discarded or escaped fish in an initial "catatonic state" in which they do not respond to stimuli may sink rapidly, and this rapid sinking may result in death from predation or physiological effects of increased pressure. Disruption of schooling and attraction of predators by visual, olfactory, and mechanical cues from injured fish, as well as from fishing vessels and gear, may significantly increase discard and escapee mortality. Other environmental factors, including light, temperature, and sea state, are also expected to control rates of predation on discards. Design of field experiments to quantify delayed mortality will be difficult. When fish were kept in sea cages after capture, predation was not present. Tag and recapture methods may include predation but cannot discriminate among causes for mortality.

Deficits in orientation, swimming ability, phototaxis, feeding, schooling, social interactions, and predator evasion have been observed in walleye pollock, sablefish, and Pacific halibut towed in a laboratory net (Olla et al. 1997; Davis and Olla 2001; Ryer 2002) or exposed to air at various temperatures (M.W. Davis, unpublished data). These behavioural deficits ultimately resulted in increased predation on fish in the laboratory that had been stressed by net towing. Although laboratory experiments are not necessarily comparable to field conditions, it is intuitively obvious that capture-impaired fish have a reduced ability to avoid predation.

Delayed mortality of discards may be reduced by allowing partial or complete recovery from capture stress before release. Although recovery tanks are difficult to use in the lim-

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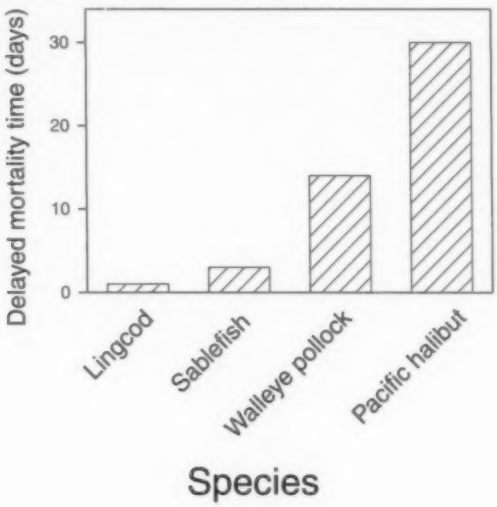
Fig. 7. Time of delayed mortality (days) in bycatch-stressed lingcod (*Ophodion elongatus*), sablefish (*Anoplopoma fimbria*), walleye pollock (*Theragra chalcogramma*), and Pacific halibut (*Hippoglossus stenolepis*) held in laboratory tanks for 60 days. Experiments and data were described by Davis and Olla (2001, 2002), Davis et al. (2001), and Olla et al. (1997).



ited space on a fishing boat in rough seas, recovery may be possible under some circumstances. A study on coho salmon (*Oncorhynchus kisutch*) caught by gill net showed that holding fish on board for a recovery period of 1–2 h may significantly reduce delayed mortality (Farrell et al. 2001).

Synthesis

Studies of discard mortality in the field have generally not addressed the importance of environmental factors and interactions of stressors in determining potential mortality rates. The focus of field studies has been to aid development of fishing gear modifications that may reduce discard mortality, e.g., mesh size, exclusion panels, grates, unhooking practices, species-selective baits, subsurface introduction of baited lines to avoid birds. In some studies, these modifications have included consideration of the behavioural interactions of fish and gear, whereas others, such as changes in trawl mesh size, have often assumed that mesh is a size-specific passive sorting device. Changes in fishing practices have been suggested to avoid areas of potential discards through the use of spatial and temporal refuges. The seemingly overwhelming economic, social, and political constraints of fisheries management seem to have precluded consideration of altering fishing practices in ways that included the effects of environmental factors.

Laboratory studies of bycatch processes have shown that environmental factors can play significant roles in discard mortality, and these results have been corroborated by a limited number of field studies. In cases where environmental factors interact with gear effects to increase mortality, changes in fishing practices could be made to reduce discard stress and mortality. Adjustments in fishing practices such as reduced trawling times or soak times for fixed gear could reduce catch (but not necessarily decrease catch per unit effort) and decrease handling times on deck. Fishing effort could be adjusted into cooler seasons of the year, or deck conditions could be moderated with shade and misted seawater. Reduced time in adverse, but nonlethal, conditions of light, temperature, air, and anoxia would certainly decrease discard stress and mortality. It is no longer sufficient to conduct discard studies in the field under a single set of conditions and expect that the results will contribute to fundamental understanding of the discard problem, either for that specific fishery or in general. The full range of fishing conditions for a gear type must be recognized and studies must include the bounds of these conditions. These study boundaries include variation in fishing practices, as well as light versus dark conditions, temperature range, time in air, anoxia, and sea state. The size-related sensitivity of discards to stressors and species differences in stress resistance are also clearly important in the management of discards.

It remains to be understood why fish die following capture and the relationship between mortality and stress physiology. Commonly measured stress factors (plasma cortisol, lactate, glucose, potassium, sodium) cannot be used to predict mortality. Because stress causes a shift from anabolic to catabolic processes, measurement of factors that control growth, such as IGF-I (insulin-like growth factor) and growth hormone, could be valuable for assessing discard fitness and mortality. Stress also could affect fitness by inhibiting the fish's immune system, either directly through the endocrine system or via energy shunting, as with growth.

How do we accomplish the goal of predicting in situ discard mortality? The combination of laboratory and field experiments is crucial to success. Laboratory experiments will be used to define the capabilities of fish to respond to classes of bycatch stressors and their interactions, with stress responses measured as changes in behaviour, physiology, growth, and immune function, as well as mortality. Then relationships can be defined between physiological variables and stress responses, including behaviour and mortality. Knowledge of these relationships would allow for prediction of direct and indirect (predation, disease) discard mortality using simple behavioural or physiological assays. In the field, discard mortality could then be predicted by sampling fish behaviour and plasma and tissue from a wide variety of fishing operations and conditions. At the same time, discard mortality predicted from in situ tagging and recapture experiments could be compared with the behavioural and physiological results as a confirmation of the prediction technique. Clearly, prediction of discard mortality in a wide range of fisheries requires fundamental knowledge of why discarded fish die and the relationships between mortality, bycatch stressors, and fish stress physiology and behaviour.

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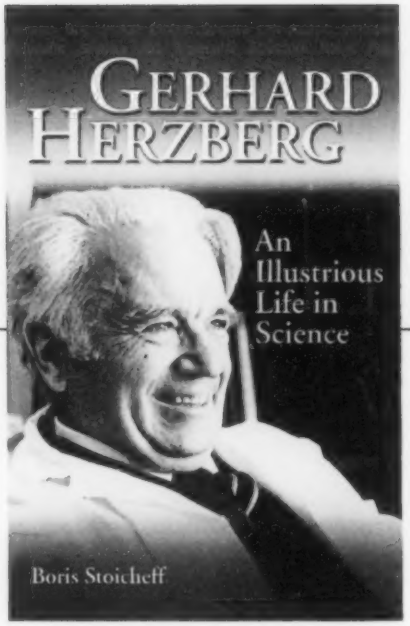

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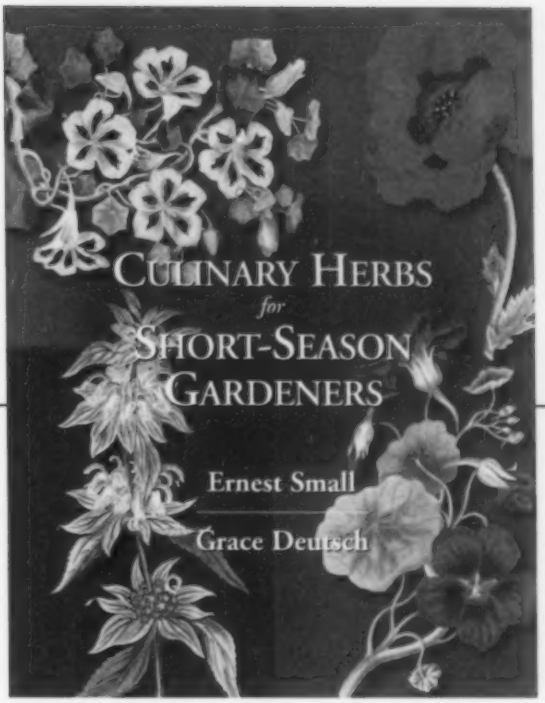

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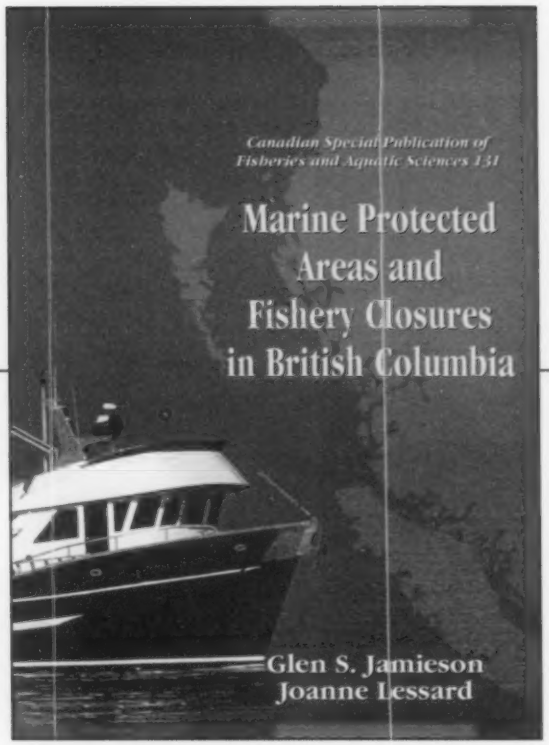
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